THE SUBFAMILY ANOMIOPSYLLINAE (HYSTRICHOPSYLLIDAE: SIPHONAPTERA). I. A REVISION OF THE GENUS *ANOMIOPSYLLUS* BAKER[1,2]

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Abstract.— In this taxonomic revision of the Nearctic flea genus *Anomiopsyllus* Baker morphological characters, phylogeny, affinities with other genera in the subfamily Anomiopsyllinae, evolutionary adaptations, geographic distribution, ecological parameters, and host preferences are discussed. Characters primarily associated with the male genitalia, in particular the number and placement of spiniforms on the movable process (finger) of the clasper, are used for species discrimination. A key to the males of the 15 species and subspecies is provided, including illustrations of both males and females.

The Nearctic genus *Anomiopsyllus* Baker is a group of small, eyeless fleas associated primarily with wood rats of the genus *Neotoma* and usually found in their nests. These fleas are characterized by the extreme reduction in the number of setae and spiny structures common to most Siphonaptera, and by the reduction and displacement of certain skeletal structures which presumably strengthen the thorax for jumping. These anatomical modifications are carried further in the genus *Anomiopsyllus* than in any other flea genus and reflect a high degree of adaptation to the nest environment.

The genus was proposed by Baker (1904) to include *Typhlopsylla nudatus* Baker, 1898. The subfamily Anomiopsyllinae was established by Baker (1905) to include *Anomiopsyllus*, which was then thought to be phylogenetically isolated and without near relatives. Since Baker's description of *nudatus*, 11 additional *Anomiopsyllus* species have been described, of which *californicus* Baker has been synonomized (Jordan and Rothschild 1915) and *congruens* Stewart has been reduced to a subspecific rank (Hopkins 1952). Traub and Tipton (1951) gave an account of the relationships of the genera within the subfamily Anomiopsyllinae, using characters found in females. Hopkins and Rothschild (1962) reviewed the seven known species and presented keys classifying all males and some females (three species and one subspecies).

While the genus has been treated adequately so far as its placement among the higher taxa is concerned, very little is known of the distribution, geographical variation, biology, or ecology of any of the species. No taxonomic evaluation using all available specimens has been made for any of the species, nor have the intrageneric relationships been analyzed. The primary purpose of this paper is to provide a taxonomic and systematic evaluation of the genus and the member species on the basis of morphological, geographical, and ecological data available from slide-mounted specimens. Distribution, host-parasite relationships, and phylogenetic relationships are also discussed.

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HOST-PARASITE RELATIONSHIPS

Species of *Anomiopsyllus* are most frequently associated with wood rats of the genus *Neotoma*; however, they have been collected occasionally from many ground-dwelling rodents, including species of *Peromyscus*, *Dipodomys*, and *Spermophilus*. There are currently three species of *Anomiopsyllus* that have not yet been associated with *Neotoma: A. oaxacae* Barnes, in which the single specimen was taken from *Baiomys musculus; A. traubi* Barrera, which is known only from a "rodent's nest"; and *A. martini* Holland, which was described from *Sciurus aberti*, a squirrel.

The rodent genus *Neotoma* Say and Ord is widely distributed in North America. The species are normally restricted to a given type of habitat varying from low, dry deserts or humid jungles to rocky slopes above the timberline (Hall and Kelson 1959). Geographical distribution of this genus ranges from Honduras and Nicaragua in Central America to British Columbia in Canada and from California east to New York and Florida in the United States.

There are 22 known species of *Neotoma* comprising 114 taxa on the species and subspecies level. Most flea species of the genus *Anomiopsyllus* are associated with wood rats, and most occur in the arid southwestern United States and Mexico where the average rainfall does not exceed 76 cm. The temperatures in these areas undergo great daily fluctuations and are generally quite high. Nest fleas are somewhat protected from ambient fluctuations because the temperature and humidity in the nest remain at a fairly constant level. Under these circumstances a nest environment may provide some selective advantages over a host environment inasmuch as a host may be away from the nest for long periods of time foraging for food and, thus, the fleas on the host would be exposed to environmental fluctuations.

DISTRIBUTION OF THE GENUS

Anomiopsyllus is exclusively Nearctic, and species have been collected in a geographical area bounded by Banff, Alberta, Canada, on the north (*A. montanus* Collins) and the state of Oaxaca, Mexico, on the south (*A. oaxacae* Barnes). *Anomiopsyllus* is restricted in the United States between the coastal range of California on the west (*A. falsicalifornicus* Fox) and the 101st meridian on the east (*A. nudatus hiemalis* Eads and Menzies). No species have been collected east of the Mississippi River, even though species of *Neotoma* do occur in the eastern United States.

GENERIC RELATIONSHIPS

Eopsylla Argyropulo is the only genus in the subfamily which occurs outside the Nearctic realm. *Eopsylla* was included in the tribe Anomiopsyllini by Hopkins and Rothschild (1962) because it is more closely related to the North American genus *Callistopsyllus* Jordan and Rothschild than it is to other Asian genera. Careful collecting in northwestern North America may reveal the presence of taxa which will further substantiate this relationship.

Genera of the Anomiopsyllinae which are exclusively North American include: *Anomiopsyllus, Callistopsyllus*, *Megarthroglossus* Jordan and Rothschild, *Stenistomera* Rothschild, and *Conorhinopsylla* Stewart. *Callistopsyllus* has the most northern distribution of these genera and is well represented in western Canada by three species (Holland 1949), two of which enter the United States by way of the Sierra-Cascade mountain chain and the Rocky Mountains. *Megarthroglossus* is also represented in Canada and extends as far south as Texas where *M. divisus* (Baker) and *M. bisetis* Jordan and Rothschild have been collected (Mendez 1956). *Conorhinopsylla* is an eastern genus and is not found further west than Kansas.

Mendez (1956) has stated that *Megarthroglossus* is more closely related to *Anomiopsyllus* than any other genus, and affinities have been shown between these genera based on comparative female characters (Traub and Tipton 1951). However, structures of the male genitalia of *Callistopsyllus* are strongly reminiscent of *Anomiopsyllus*, especially with regard to the clasper and its movable process. The articulation of the movable process in *Callistopsyllus deuterus* Jordan is very similar to that of *A. amphibolus* Wagner and *A. montanus*; the process resembles that of *A. amphibolus*, both in shape and in the presence of two spiniforms. The aedeagi of all three genera have much in common. However, the aedeagus of *Anomiopsyllus* is reduced and has no prominent dorsal or subterminal lobes. The affinities of *Conorhinopsylla* and *Stenistomera* with the rest of the Anomiopsyllinae are also borne out by similarities in male genitalia.

Both distributional and morphological evidence indicate that *Anomiopsyllus* is a member of a monophyletic group, and that the genus has evolved in North America from an ancestor common to other members of the Anomiopsyllinae. *Anomiopsyllus* is more closely related to both *Callistopsyllus* and *Megarthroglossus* than to either *Stenistomera* or *Conorhinopsylla*. In all probability, *Anomiopsyllus* has evolved exclusively in North America in conjunction with the Nearctic genus *Neotoma*, its wood rat host.

SKELETAL ANATOMY OF ADULTS

The remarkably reduced nature of some structures in *Anomiopsyllus* has evoked comment from every author discussing the genus, and in two instances (Ewing and Fox 1943, Hubbard 1947) the genus has been included in the Pulicoidea rather than in the Ceratophylloidea where it was rightfully placed by Jordan and Rothschild (1915). The past taxonomic confusion has undoubtedly resulted from loss of the more obvious distinctive characters typical of Ceratophylloidea, which has brought about a superficial resemblance of *Anomiopsyllus* and the Pulicoidea.

The outstanding features of *Anomiopsyllus* anatomy include complete eyelessness, an extreme reduction in number of setae and spines, extensive loss and fusion of structures in the metathorax, and loss of structures in both meso- and metacoxae. In contrast to the highly modified nature of the thorax, the abdominal segments are only moderately specialized, though marked by loss of some structures in the male genitalia. Of these characters, eyelessness has arisen in a number of widely separated genera and seems to be associated with nest dwellers (Traub 1953).

Reduction in setation in Siphonaptera has been carried to its greatest extreme in *Anomiopsyllus*. Loss of setae and of important spines undoubtedly has great adaptive as well as taxonomic significance. The adaptive significance of such losses is not clear because several highly successful nest fleas which are in some respects as specialized as *Anomiopsyllus* (e.g. *Stenistomera*) have gone in the opposite direction by developing numerous large setae.

In the following section, the more fundamental aspects of *Anomiopsyllus* anatomy are emphasized, especially those in which the genus differs from its relatives and those which would seem to have clear adaptive significance. Snodgrass (1946) has dealt extensively with the skeletal anatomy of fleas; his terminology and interpretations are used here as a basis of comparison.

HEAD

Fig. 1

The head capsule is oval in shape, but its outline is broken anteriorly by a well-defined clypeal tubercle. There is no interantennal suture. The eyes are completely lacking, as in *Callistopsyllus*; the allied *Megarthroglossus* has vestigial eyes.

The degree of sexual dimorphism in antennal size and shape is striking. The small, oval antennae of the female do not reach the prosternum. The male antennae are greatly lengthened with their bases higher up on the head capsule and their apices extending back upon the prosternosome on which the antennal fossae are continued. Though deep, the antennal fossae as seen in a posterior view of the head capsule do not meet in the interior of the head capsule, nor are they connected by a trabeculum.

The mouthparts bear no structures not duplicated elsewhere in Siphonaptera. The extended members are long in proportion to the remainder of the flea and reach the trochanter of the procoxae. The labial palpi are 4-segmented, and the stylets are armed their full length with minute, laterally placed nodules. The epipharyngeal stylet is completely unarmed, as illustrated by Snodgrass (1946) for *Opisodasys* Jordan, and is unlike those of *Hystrichopsylla* Taschenberg and others which bear teeth.

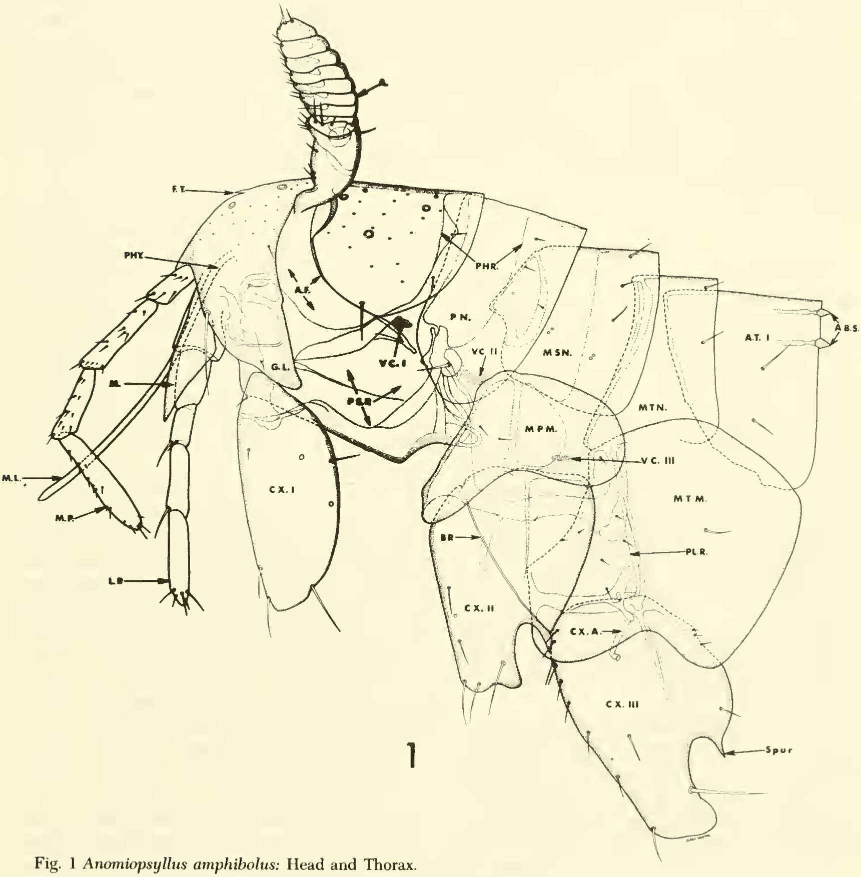


Fig. 1 *Anomiopsyllus amphibolus:* Head and Thorax.

The anterior tentorial arms remain complete and extend from a point near the tentorial bridge to connect anteriorly near the genae. Snodgrass suggested that these arms are in reality the dorsal tentorial arms since true anterior arms arise in the clypeal area. The completeness of these arms and lack of a trabeculum centralis are considered by Johnson (1957) to be primitive characters associated with the Hystrichopsyllidae. In the Ceratophyllidae, the anterior arms are in the process of being lost and replaced by the trabeculum.

In its remarkable antennal sexual dimorphism, *Anomiopsyllus* is highly advanced within the Hystrichopsyllidae, in which the more primitive members show little difference in this regard between the male and female. Within the Anomiopsyllinae all genera show some degree of sexual dimorphism, but of the genera examined *Anomiopsyllus* and *Callistopsyllus* show the greatest antennal enlargement.

Thorax

Fig. 1

Structurally, the thorax is characterized by the total lack of the pleural arch and an extreme degree of fusion in the metathoracic segments. The pronotal comb is absent, and setae are reduced both in number and size.

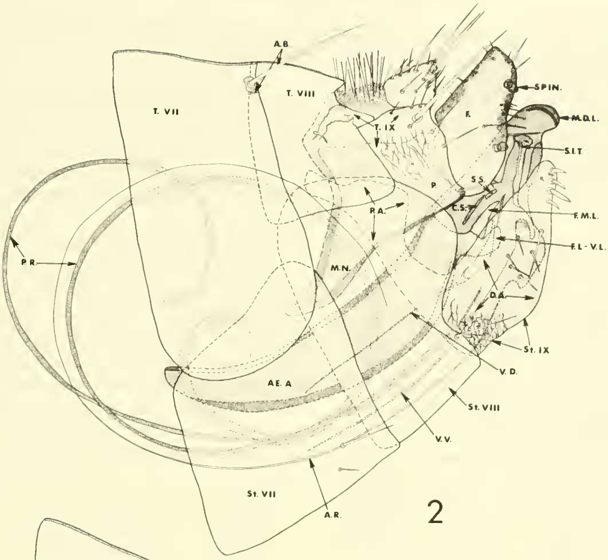
The prothorax, aside from the absence of the pronotal comb, is not remarkable. The fused pleurosternal plate is not divided into the proepisternum and proepimere by a ridge as in *Hystrichopsylla*. The ventral margin of this plate is straight with the dorsal margin sinuously downcurving caudally; thus, the plate is broader anteriorly than posteriorly. The caudal margin of the free flange of the pleurosternum is relatively straight except for a small, sharp, median triangular projection. The pronotum is a simple, collarlike sclerite.

There is considerable disagreement among authors concerning the structure of the sternal and pleural areas of the meso- and metathorax and of the lateral notal and episternal areas of the metathorax. Snodgrass (1946) considered the sternum to consist of a narrow strip lying between the coxae and fused with the episternum anteriorly, leaving the posterior portion of the sternum as a free arm. Jordan (quoted in Hopkins and Rothschild 1953) considered the sternum to have lateral elements fused to the episternum. This divergence in viewpoint confuses terminology: the episternum of Snodgrass is considered the sternum (at least in part) by Jordan; the lateral metanotal area of Snodgrass is considered the episternum by Jordan.

Johnson (1957) follows the interpretation of Snodgrass, whose terminology is used here, and presents additional evidence for its support. She points out that the ventral margin of the episternum in both the meso- and metathorax ends in a free flange and that the sterna are entirely separate from the episterna except where fused anteriorly. The free flanges of the episterna appear not only to extend below the sterna, but also to overlap a portion of the coxae.

The mesothorax of *Anomiopsyllus* is relatively unmodified (Fig. 1). The notum is simple with the anterior phragma large and prominent in slide-mounted specimens. It is marked by the complete loss of internal pseudosetae beneath the mesonotal collar. These pseudosetae are found in other anomiopsyllines and differentiate the Ceratophylloidea from Pulicoidea. The mesepisternum and mesepimere are separated by a strong vertical pleural rod, firmly attached at both ends. This rod supports the pleural articulating sclerites of the coxa. The ventral margin of the mesepisternum curves downward and anteriorly from the base of the pleural rod, forming a free flange slightly overlapping the coxa and fusing anteriorly with the sternum. The ventral margin of the mesepimere is relatively straight. The mesepimere forms a free caudal flange,slightly overlapping the metepisternum near the point of attachment of the third link-plate or vinculum. Dorsally, it slightly overlaps the ventral edge of the mesonotum except at the anteriormost corner.

The metathorax of *Anomiopsyllus* (and all other Anomiopsyllinae) is marked by extreme fusion and a rather radical displacement of parts. The net effect is anterior fusion of the notum with the



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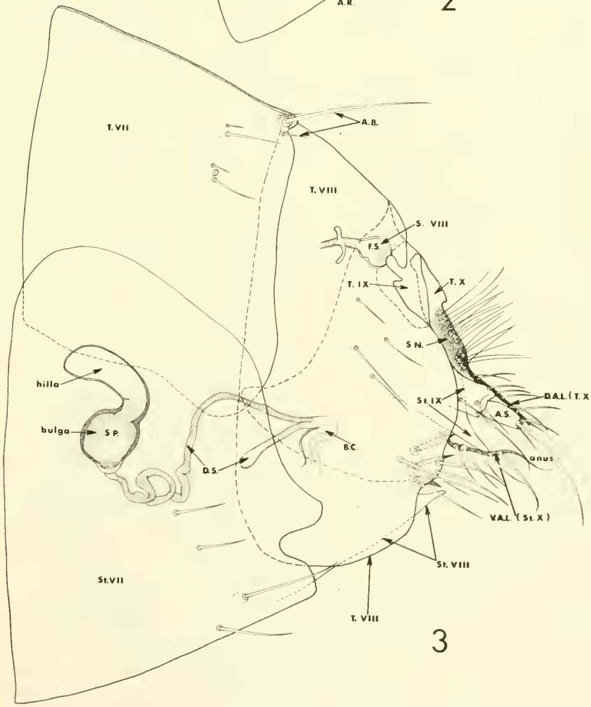

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Figs. 2-3. *Anomiopsyllus amphibolus:* 2, male terminalia; 3, female terminalia.

metepisternum, loss of the lateral metanotal area, and loss of the pleural arch. These complex phenomena have been subject to some discussion by taxonomists, particularly Johnson (1957), and warrant further discussion and clarification, especially with regard to the mechanics involved, evolutionary trends, and possible adaptive significance.

In order to understand what has taken place in the metathorax, it is necessary to review the work of Snodgrass (1946), especially with regard to the strengthening rods and lateral metanotal area.

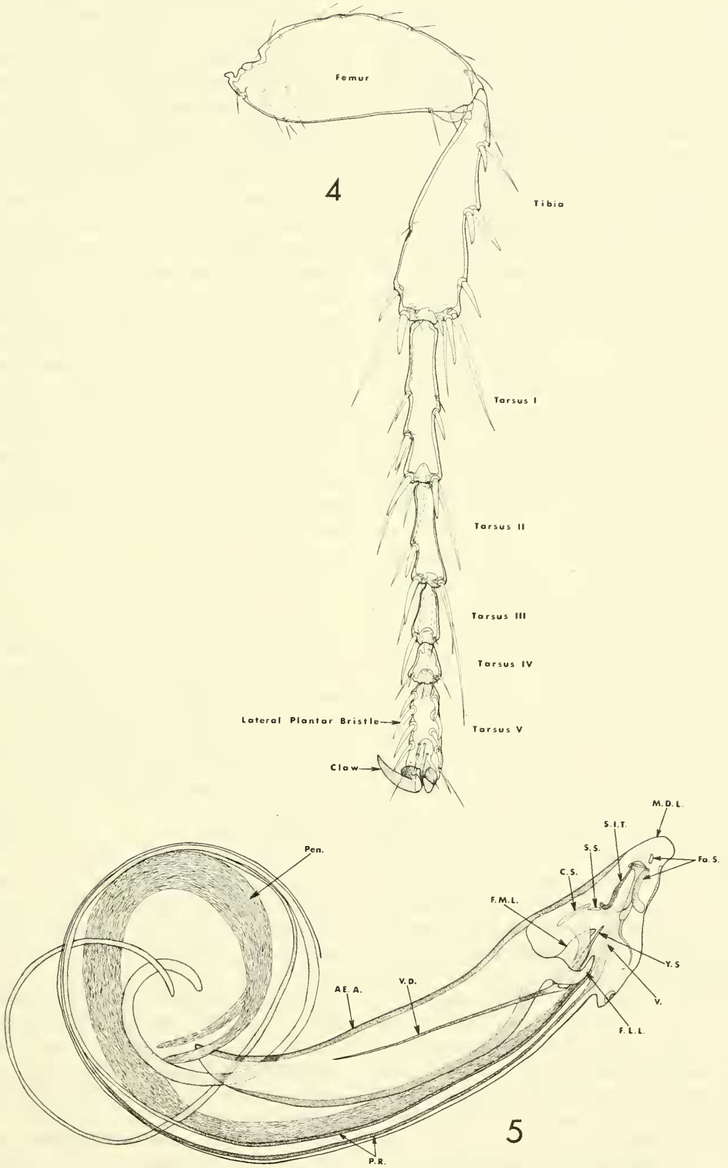
In most fleas, the metanotum is a collar-shaped structure. It normally bears two transverse strengthening ridges, the anterior prephragmal ridge and the more posterior notal ridge. Near the lower end, the transverse notal ridge gives off anteriorly a short longitudinal ridge which usually continues to the anterior edge of the notum where it blends into a marginal thickening continued around the ventral edge of the notal plate. The accessory ridge thus sets off a small, variously shaped ventrolateral area of the metanotum, termed the lateral metanotal area (see Snodgrass, Pl. 8., Figs. K-O; Pl. 9, Figs. A-E). This area normally bears a small but distinct, free marginal flange, but in *Pulex* it is fused with the upper margin of the metepisternum. Contrary to the findings reported by Johnson (1957), *Pulex* still retains the lateral metanotal area: though fused with the metepisternum, it is still set off by the ventrolateral thickening extending from the lower anterior margin to the ventral extension of the notal ridge.

The notal flange normally extends into the pleural area, where it terminates in an oval expansion that overlaps and clasps the upper end of the pleural rod, thus forming the so-called pleural arch (see Snodgrass, 1946: 26, Pl. 9, Figs. C, H-K). The union is a very firm one. Snodgrass states (p. 26): "It is evident, therefore, that this apparent notopleural 'articulation' of the metathorax is for the purpose of solid union along the line of the notal and pleural ridge, and is not for controlled movement. The flexibility of the united ridges allows the pleuron to be twisted somewhat on the notum, but *permits of no swinging* movement in a longitudinal plane."

According to Snodgrass, *Opisodasys* and *Dactylopsylla* Jordan possess a pronounced posterior angulation between the notal flange and the axis of the pleural ridge. This condition applies in *Orchopeas* Jordan and most ceratophyllids. In these fleas, the pleural ridge has moved anteriorly to the line of the notal flange and is fused strongly to its angled ventral extension.

In *Anomiopsyllus* and allies, much more radical changes have taken place. In *Anomiopsyllus, Megarthroglossus, Callistopsyllus,* and *Stenistomera*, the notal ridge is strongly reduced in thickness and extent and the lower portion has disappeared above the notal margin. The accessory ridge is still present; its identity is established by the attachment of the link-plate or vinculum at its anterior end (Fig. 1, VC. II). This ridge is strongly developed anteriorly, but fades posteriorly to varying degrees in the anomiopsyllines examined, and does not meet the ventral remnant of the notal ridge. The ventral extension of the notal ridge is apparently gone. The long metapleural rod has been displaced anteriorly and is apparently completely fused with the accessory ridge. There is no sign of a pleural arch. Along with this, the metepisternum and metanotum are completely fused, and in *Anomiopsyllus* there is no vestige of the lateral metanotal area.

A clue to what has happened is present in *Megarthroglossus*, and perhaps in *Stenistomera* and *Callistopsyllus*. In *Megarthroglossus* a small thickening leads anteriorly from the upper portion of the pleural rod, but ends before it reaches the anterior margin of the segment. Its position suggests that it represents the vestigial ventral thickening of the lateral metanotal area. A similar thickening exists in the other genera, but leads posteriorly from the anterior margin. In *Stenistomera* the thickening is short and knoblike and in *Callistopsyllus* it is longer. If the structure in *Megarthroglossus* is indeed, as suggested, part of the "pleural rod," it must represent the ventral portion of the notal flange, which has completely fused with the pleural rod. The notal flange



Figs. 4-5. *Anomiopsyllus amphibolus:* 4, metathoracic leg; 5, aedeagus.

has lost its direct connection with the notal ridge proper and has been displaced anteriorly with the pleural rod. This would be correct, since the ventral thickening of the lateral metanotal area always connects with the ventral extension of the notal ridge in those fleas that possess the lateral metanotal area. In the ceratophyllid genus, *Orchopeas*, and perhaps others, we see a forward angulation of the ventral end of the notal ridge and an anterior displacement of the pleural rod, but the elements essential to the pleural arch are present and highly developed. In *Anomiopsyllus* and allies these structures have been entirely lost or have lost identity by fusion.

Johnson (1957:8) has offered an explanation of the adaptive significance of the loss of the lateral metanotal area and the pleural arch. According to her, the pleural arch serves as a strengthening device which acts as a "cushion" in jumping. Since *Anomiopsyllus* is a "nest flea" and consequently a "poor jumper," the pleural arch is no longer necessary. She explains the means by which it was lost as "... probably loss due to lack of selection against any mutation tending toward reduction of the pleural arch which, if my premise is correct, is mainly an aid in jumping."

The negative view that such a radical change involving major structures has arisen by mutations in the absence of selection pressures is difficult to accept. Such phenomena undoubtedly occur in isolated island populations where the gene pool is small and selection pressure slight, but they must be exceedingly rare in any continental group. In a rigorous continental environment, one would not expect mutations to survive in the absence of some positive selective advantage to the mutant. One must postulate that any such radical change would have to offer a positive selective advantage to be retained. Losses which may take place by mutation in the absence of selection could be termed degenerative evolution. Thus, *Anomiopsyllus* may be dubbed a "degenerative form," a term disapproved of by Johnson (1957:16).

The possible selective advantage of the anterior displacement and fusion of strengthening ridges in the metathorax of anomiopsyllines may be partially clarified by observations of adult fleas in the laboratory under both artificial and near-natural conditions. *Anomiopsyllus* is not a weak jumper. It does not jump at all! *Callistopsyllus*, *Megarthroglossus*, and *Stenistomera* are weak jumpers. This is probably due in part to correlated differences in meso- and metathoracic coxae as well as to changes in the metathorax. This becomes apparent with microscopic observations of flea movements through tangles of nest material. The abdomen of *Anomiopsyllus* is capable of sweeping movement *in the lateral plane* as the flea moves through nest material with a rapid, sinuous movement. Lateral flexibility is not observable in the more rigidly constructed *Hystrichopsylla* and *Atyphloceras* Jordan and Rothschild. Anterior displacement of thoracic ridges and reduction of the notal ridge offer a considerably greater degree of flexibility in the metathorax.

LEGS
Fig. 4

The legs of *Anomiopsyllus* are marked by prominent posteroapical sinuses on both meso- and metacoxae, above which are large subacuminate spurs (Figs. 1, SPUR). The prolegs are not distinctive. The mesocoxae possess a complete longitudinal break (Fig. 1, BR.), considered to be an advanced condition. A complete break is also found in *Megarthroglossus*, but not in *Callistopsyllus* or *Stenistomera*. This condition also is found among the Rhadinopsyllinae. In an anterior view, the mesocoxae are seen to fold inward at the break, forming a shield similar to that formed by the procoxae, as described by Snodgrass (1946). The shield is formed by pivoting the procoxae at the pleurocoxal articulations. Snodgrass postulated that the "shield" formed by the procoxae may be useful for forcing between hairs or may be used as a flat base for feeding. The second "shield" formed by the mesocoxae in *Anomiopsyllus* and *Megarthroglossus* suggests the former explanation and perhaps is needed to cope with the greater heterogeneity and density of nest material rather than hairs on the host.

In *Anomiopsyllus* and other anomiopsyllines, the exterior coxal ridge in both meso- and metacoxae is incomplete. In those fleas examined by Snodgrass (1946), including *Pulex* Linnaeus, *Hystrichopsylla*, *Dactylopsylla*, and *Opisodasys*, and in most other fleas, the ridge is complete and reaches the apex of the coxae. The meso- and metacoxae are articulated mesally to the sternum by a pair of prominent articulating sclerites (Fig. 1, CX. A). The upper mesal coxal surface is membranous, and the articulating sclerites serve as the only rigid connection between sternum and coxae. These sclerites normally articulate with a well-defined socket in the dorsal edge of the mesal sclerotized surface of the coxa. At the point of articulation, the coxa is strengthened by a horizontal thickening and a longitudinal rod extending toward the coxal apex (see Snodgrass 1946) and may or may not reach the apex of the coxa. This structure has been termed the mesal coxal ridge by Snodgrass. In *Anomiopsyllus*, there is no hint of thickening at the point of articulation and the rod is entirely absent. Both thickening and rod are present in the related genera *Callistopsyllus*, *Megarthroglossus*, and *Stenistomera*.

The reduction of the coxal ridge, absence of mesocoxal ridge, and complete mesocoxal break in *Anomiopsyllus* would seem to be further examples of specialization to the nest environment and to walking rather than jumping.

ABDOMEN

The unmodified abdominal segments (I-VI) are not remarkable except for the characteristic reduction in number and size of setae. Terga I and II each bear spinelets at the apical margin, the former usually 2 per side, the latter 1. Each tergum bears a row of thin setae, 3 to 5 on each side, plus 1 very minute guard seta below and anterior to each spiracle. Sterna II to VI are simple, usually bearing two setae ventrally, the upper one usually the longer.

Modified abdominal segments of males (Fig. 3): Segment VII is the first modified segment. The tergum bears one long antepygidial seta which is not reduced or altered in shape. Sternum VII is not modified differently from preceding sternal segments. Sternum VIII is expanded posteriorly and dorsally to serve as the chief ventrolateral shield about the genitalia and differs markedly from the more anterior segments. The tergum is marked at the posterior margin by rather prominent setigerous grooves containing the spiracles below which it expands caudally to serve as the main dorsolateral shield for the genitalia. It is comparatively shallow, descending ventrally only about half the distance of the preceding terga. Sternum VIII closely resembles that of the other Anomiopsyllinae by being expanded and ensheathing much of the proximal portion of sternum IX.

Segment IX of males (Fig. 3) is exceedingly modified; included in its structure is the clasping apparatus of the external genitalia. Its tergum is much reduced dorsally and consists of a narrow but complete strap anterior to the pygidium (Figs. 3-4, T. IX). The tergum is continuous with the upper anterior angle of the clasper lobes, very much as noted for *Hystrichopsylla* by Snodgrass (1946). Immediately below and anterior to the tergal strap is a small but strong tergal apodeme, reinforced by thickened bars that join the anterodorsal angles of the large manubria (Figs. 3, MN). The apodeme forms a strong dorsal arch between the manubria at this point from the anterior edge of the dorsal arch. The anterior margin descends downward into the abdominal cavity, then curves dorsally and posteriorly to join the clasper lobe, thus forming a prominent triangular structure.

The tergal clasping apparatus consists of the broadened clasper lobe composed of a more or less dome-shaped fixed process (P) and an articulated movable process (F). The fixed process is usually equipped at or near the apex with a long, heavy bristle projecting over the apex of the movable process (lacking in *A. novomexicanensis*). Invariably, the movable process or "finger" is equipped with heavily pigmented, large spiniform setae on the mesal surface. The number and position of these setae have been used extensively in taxonomy. The posteroventral apex of the clasper lobe below the articulation of the movable process bears the acetabular seta. The articulation of the movable process is on the *inner* surface of the clasper lobe. The socket may be oval or nearly round (as in *nudatus*, *novomexicanensis* and *falsicalifornicus* groups) or linear and nearly vertical (as in the *amphibolus* group).

Sternum IX (Fig. 3) consists of two main components, the proximal and distal arms. Together, in lateral view, they form a prominent V-shaped structure easily seen in slide-mounted specimens. The proximal arms are platelike sclerites, characteristically shaped in some species but variable enough that taxonomic value is limited. In *Anomiopsyllus*, they extend dorsad and anterad almost to the anterodorsal angle of the manubrium. The distal arms form a single troughlike structure from the base to a point 20 to 25 percent of the distance from the apex, after which they separate and are free. The heavily reinforced lateral portions are interconnected by a more lightly sclerotized, distally convex median plate variously adorned by setae. The pattern is characteristic of the species. The apices of the free arms are equipped with large, tacklike setae. Their number and size are of taxonomic value. In some species, there is a lobe which forms a narrow sheath around the angle of the distal arm about three-fourths of its length. In others, this structure is greatly reduced and difficult to see.

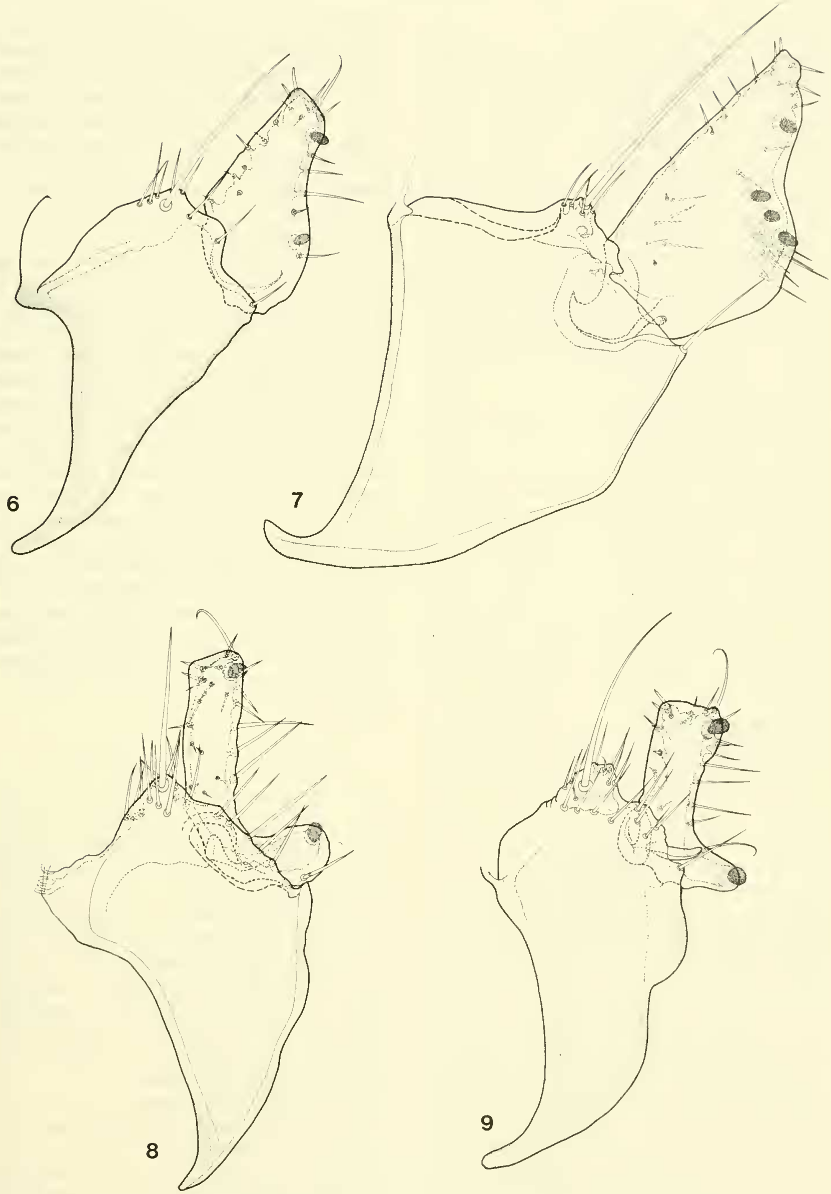
AEDEAGUS (Fig. 5): The aedeagus of *Anomiopsyllus* is simple and basically very similar to that of *Hystrichopsylla dippiei* Rothschild, as described by Snodgrass (1946) and Traub (1950). It is long and narrow. The apodeme is broadly scimitar shaped with a prominent basal constriction or neck. The endchamber is a simple hood opened apically and ventrally. The crochets (CR) are reduced and immovable in the ventrolateral wall. The aedeagal pouch is deep, extending considerably cephalad of the struts. The sclerotized inner tube (S.I.T.) is prominent, tubular, and funnel shaped at the base with a prominent anteroventral spur to which is attached the apodemal rod. The crescent sclerite (C.S.) of *Anomiopsyllus* is prominent and attached to the anterodorsal flange of the tube. Penis rods are long and coiled. There are no specialized lobes present, indicating its primitiveness as compared to ceratophyllids and pulicids.

MODIFIED ABDOMINAL SEGMENTS OF FEMALES (Fig. 2): Tergum VII bears the single, long antepygidial bristle. Sternum VII is marked by a posterior expansion with its margin shaped variously in the several species. The upper margin of sternum VII, as pointed out by Snodgrass (1946), overlaps its tergum (Fig. 2, St. VII).

Segment VIII is exceedingly modified. The tergum consists of two lateral plates narrowly joined dorsally, expanding ventrally and posteriorly to cover most of the genitalia. Its posterior margin near the dorsum contains the deep setigerous grooves of the most posterior spiracle. From that point, it expands posteriorly. The most posterior margin may be straight or lobed (Fig. 2, T VIII), depending on the species. Its usefulness as a taxonomic character is reduced by intraspecific variation. Sternum VIII, as in other fleas, is reduced to a small plate between the two valves of its tergum and functions only as the ventral floor below the genitalia.

Tergum VIII completely encloses the external genital chamber and is guarded at its orifice by a group of very heavy, inward-directed mesal setae. The lateral walls of the genital chamber are heavily sclerotized in *Anomiopsyllus*, apparently forming a channel. The bursa copulatrix is a simple sack at or near the anterior end of the "channel." The bursa, in some species, (notably *novomexicanensis* Williams and Hoff, Fig. 90) has minute areas of sclerotization, and in others it appears as a wholly membranous sack. The spermatheca is simple, with a more or less globular bulga (head) and a curving, broad hilla (tail) without a terminal appendage (Fig. 2).

Segment IX in *Anomiopsyllus* is marked by well-developed tergal plates. As pointed out by Snodgrass (1946: 36), segment IX of most female fleas is virtually obliterated. Those groups retaining well-developed tergal plates on this segment include: *Hys-*



Figs. 6-9. Finger and clasper: 6, *Anomiopsyllus amphibolus*; 7, *A. nidiophilus*; 8, *A. montanus*; 9, *A. sinuatus*.

trichopsylla (Snodgrass 1946); *Ctenopthalmus* Kolenati, 1956; *Parapsylla* (Wagner, 1939); and *Atyphloceras* Jordan and Rothschild, 1915. *Anomiopsyllus* is suggestive of the more primitive hystrichopsyllid genera in the retention of a well-developed tergum IX. These plates consist of teardrop-shaped valves on either side of the pygidium, well rounded dorsally, ventrally, and anteriorly but acute posteriorly with points projecting beyond the anus, below the anal stylets, and outside the anal plate (Fig. 2, 3, T. IX). From the dorsal aspect, the plates appear to be joined anteriorly only by a membranous connective and are completely separated from tergum X by a suture.

Segment X contains the prominent pygidium, the proctiger, and the anus. The pygidium is framed by a narrow, strongly sclerotized ring somewhat open anteriorly but joined by a small plate. It bears 20 (10 per side) sensillial pits (Fig. 2, SN.), though 21 were noted on one specimen of *A. f. congruens* from Placerville, California. The number of sensillia is used as a key character by Hopkins and Rothschild (1956) to separate Pulicoidea from Ceratophylloidea. According to them, pulicoids bear 8 to 14 sensillial pits per side and ceratophylloids sometimes bear 14 but usually bear 16 or more. The reduced number of these pits in *Anomiopsyllus*, a definite ceratophylloid in other respects, is interpreted here as an example of convergence through loss and does not indicate pulicoid affinities. The proctiger (Fig. 2, DAL.) is prominent and well endowed with strong setae. The anal stylets are simple and equipped with one long terminal seta and one or two minute subterminal setae.

DISCUSSION

The skeletal anatomy of *Anomiopsyllus* is most marked for its extreme reduction of parts and small size. This reduction has been accompanied in *Anomiopsyllus* by the loss of a number of behavioral characteristics common to fleas, particularly the ability to jump. Undoubtedly these reductions are adaptations to its role as a nest flea, with *Anomiopsyllus* progressing further than any other flea group. The loss of the pleural arch and the moving forward of the pleural rod reduce the mobility of *Anomiopsyllus* as far as jumping is concerned, but probably enable the flea to move through heterogeneous nest material at a more rapid rate. Modifications of the mesocoxae probably also serve this purpose.

With respect to both male and female modified abdominal segments, *Anomiopsyllus* has retained the basic structure of its more primitive relatives in the Hystrichopsyllidae. The aedeagus, for example is far less complex than that of any ceratophyllid or pulicid, and less complex than that of the other Anomiopsyllinae, including *Callistopsyllus* and *Megarthroglossus*, to which it is most closely related. Nevertheless, the relationships of the aedeagus of *Anomiopsyllus* to those of its hystrichopsyllid relatives are made clear by comparison with that of *Hystrichopsylla*. In the female, retention of the ninth tergal plates further links *Anomiopsyllus* to its more primitive hystrichopsyllid relatives. The reduction in the total number of sensillial pits on the pygidium represents specialization, probably accompanying overall reduction in size.

CHARACTERS USED IN THE STUDY

The differences between *Anomiopsyllus* species and, to an even greater extent, between subspecies are found almost entirely in the male external genitalia. Few tenable characters are available in females. For the most part, differences in configuration of sternum VII of females serve only to separate species groups. Configuration of the posterior margin of tergum VII used by Hopkins and Rothschild (1962) to separate species in their key does not hold when long series are studied, though trends may exist in any given population.

In males, particular attention has been given structures of the ninth abdominal segment, which is modified to form the clasping apparatus of the external genitalia. The shapes of the movable and immovable processes are somewhat variable within species, but are nevertheless stable enough to constitute good species characters. Consistent differences in these structures also serve as species group characters as does the structure of the articulation of the movable process. Arrangement and number of setae of both the movable and immovable processes of the clasper serve as species and subspecies characters. In some of the species one of the prominent spiniforms of the movable process seems to be in the process of being lost and is absent in some specimens. Differences in the shape and setation of the distal arm of sternum IX are useful at the subspecific level and more so at the specific level. The general shape of the proximal arms of sternum IX is useful as a secondary character at the species level, but varies a great deal in detail and is not usable in determining subspecies. Among several subspecies the distance between prominent spiniform setae has proven to correlate well with other characters, including geographic distribution. The aedeagus varies less than do other structures of the genitalia; nevetheless, some variation does occur in configuration of the dorsal margin and in dimensions. These are of some use at the species level.

LIST OF ABBREVIATIONS

A.	Antennae
A.F.	Antennal fossa
AE.A.	Aedeagus apodeme
A.B.	Antepygidial bristles
A.R.	Apodemal rod
A.S.	Anal stylet
AB.S.	Abdominal spinelets
A.T.I	Abdominal tergum I
B.C.	Bursa copulatrix
C.S.	Crescent sclerite
CX.A.	Coxal anticulating rod
CX. I	Coxa I (Pro)
CX. II	Coxa II (Meso)
CX. III	Coxa III (Meta)
D.A.	Distal arm of Sternum IX
D.A.L. (T.X.)	Dorsal anal lobe (Tergum X)
D.S.	Duct of spermatheca (Ductus seminalis)
F.	Finger (movable process) of clasper
F.L.L.	Fulcral lateroventral lobe
F.M.L.	Fulcral median lobe
FO.S.	Ford sclerite
F.S.	Fossa spiracular
F.T.	Frontal tubercle
G.L.	Genal lobe
L.P.	Labial palp
M.D.L.	Median distal lobe of aedeagus
MSN.	Mesonotum
MTN.	Metenotum
M.L.	Maxillary lacinia
MN.	Manubrium
M.P.	Maxillary palp
MPM.	Mesepimeron
MTM.	Metepimere
M.	Maxilla
P.	Process (immovable) of clasper
P.A.	Proximal arm of Sternum IX
PHR.	Phragma
PHY.	Pharnyx
PN.	Pronotum
PEN.	Penis
P.R.	Penis rods
PL.R.	Pleural rod
PSP.	Pleurosternal plate
SP.	Spermatheca
SN.	Sensillium
S.I.T.	Scleritized inner tube
SPIN.	Spiniform
S.S.	Satellite sclerite
ST. VII	Sternum VII
ST. VIII	Sternum VIII
ST. IX	Sternum IX
T. VII	Tergum VII
T. VIII	Tergum VIII
T. IX	Tergum IX
V.	Vesicle
V.A.L. (St. X)	Ventral anal lobe (Sternum X)
VC. I	Vinculum I (Link-plate I)
VC. II	Vinculum II (Link-plate II)
V.D.	Virga dorsalis
Y.S.	"Y" sclerite

SYSTEMATIC SECTION

Anomiopsyllus Baker

Anomiopsyllus Baker, 1904, Proc. U.S. Nat. Mus. 27: 377 (Type Species: *Typhlopsylla nudata* Baker, 1898.); Oudemans, 1909, Nov. Zool. 16: 157; Jordan and Rothschild, 1915, Ectoparasites 1: 45; Dalla Torre, 1924, Natur. Med. Ver. Innsbruck 39: 17; Ewing, 1929, Manual of Ectoparasites: 162; Jellison and Good, 1942, Index to the literature of Siphonaptera of North America: 21; Ewing and I. Fox, 1943, U.S. Dept. Agric. Misc. Publ. 500; Costa Lima and Hathaway, 1946, Monogr. Inst. Oswaldo Cruz 4: 522 pp.; Hubbard, 1947, Fleas of western North America: 56, 78; Holland, 1949, Siphonaptera of Canada: 96; Eads and Menzies, 1950, Fleas of Texas; Anon., 1950 (a & b), Public Hlth. Repts. 65: 454, 526; Traub and Tipton, 1951, J. Wash. Acad. Sci. 41: 267-268; Wiseman, 1955, Univ. Wyo. Publ. 19: 28 pp.; Finley, 1958, Univ. Kans. Publ. Mus. Nat. Hist. 10: 213-522; Parker and Howell, 1959, J. Parasitol. 45(6): 507-604; Stark, 1959, Siphonaptera of Utah; Vargas, 1960 Med. Rev. Mexicana 40 (849): 1; Kartman et al., 1960, Zoon Res. 1(1): 178; Hopkins and Rothschild, 1962, Catalogue of the Rothschild Collection of Fleas III: 392; Holland, 1965, Canadian Ent. 97: 1051-1058; Jellison and Glesne, 1967, Index to the literature of Siphonaptera of North America, Suppl. 2: 13-19; Tipton and Mendez, 1968, Pacific Insects 10(1): 179-182; Beck and Allred, 1966, Brigham Young Univ. Sci. Bull., Biol. Ser. 7(2): 13; Stark and Kinney, 1969, J. Med. Ent. 6(3): 290; Pratt and Stark, 1973, DHEW Publication 74-8267: 11; Lewis, 1974, J. Med. Ent. 11(2): 154.

Anomiopsylla (sic): Augustson and Durham, 1961, Bull. South. Calif. Acad. Sci 60(2): 100.

Anomiopsyllus is immediately separable from other Anomiopsyllinae by extreme reduction in number and size of setae, lack of a pleural arch, and absence of a pronotal comb and from *Eopsylla* by the lack of internal mesonotal setae (Hopkins and Rothschild 1962).

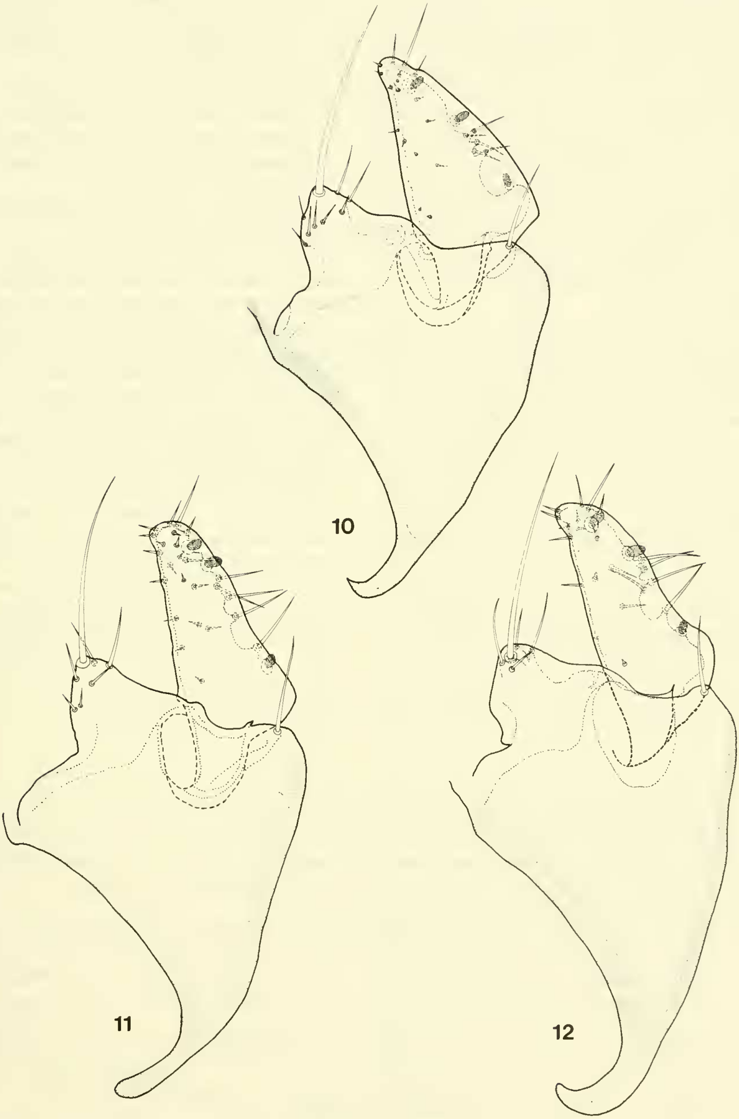
Head.— Rounded anteriorly, clypeal tubercle present, prominent; eyes absent; trabecula centralis absent; labial and maxillary palpi 4-segmented, reaching to or slightly beyond protrochanter; terminal segment of labial palpi not markedly asymmetrical nor greatly longer than other segments; maxillae acutely triangular, somewhat convex anteriorly; concave posteriorly, genal lobe broadly rounded, short. Antennae of male much enlarged, antennal fossae of males beginning almost at dorsal margin of head, connected dorsally by a falx; second antennal segment not overlapping base of third; antennal setation sparse, short, setae of female second antennal segment only one-fourth length of clava. Frons with one row of setae; occiput with a row of minute setae; antennal fossa with several setae along posterior margin.

Thorax.— Pronotal comb absent, pseudosetae absent. Pleural arch absent. Metepimeron partially fused with metanotum, latter with a small, free posteroventral flange. Metepisternum completely fused with metepimeron and anterior portion of metasternum. Posterior margin of mesocoxa and metacoxa deeply emarginate preapically, forming a deep sinus and sharp preapical spur, mesocoxa with a prominent longitudinal break from anterior base to preapical posterior sinus. Coxae, femora, and tibiae with few or no lateral setae, procoxae with row of long, thin setae on posterior margin. Femora and tibiae with weak posterior marginal setae, meso- and metafemora and tibiae with few very weak anterior marginal setae. Tarsi with four lateral pairs of plantar bristles, the basal pair moved ventrally on the pro- and mesotarsi.

Abdomen.— Terga with one row of weak setae; tergum I with two to four apical spinelets; tergum II with one or two. Abdominal sterna each with two slender, ventral submarginal setae. One antepygidial bristle in both sexes.

Female.— Tergum VIII posterior margin sloping posteroventrally, then ventrally to enclose the genitalia. Genital chamber marked by heavily pigmented area on tergum VIII, its gonotreme protected by four to six heavy, distomesad setae, forming an "ovipositor." Tergum IX large, broadly curving laterad around pygidium and proctiger, tapering to an acute point posterolaterad near anal stylet. Anal stylet approximately 2.0 to 2.5 times as long as broad, with long, slender, curving terminal seta and one minute preapical, subdorsal seta. Anal plate broad at base, dorsal margin linear, ventral margin gently curving to point.

Male.— Tergum IX narrow but entire dorsally with a well-developed tergal apodeme forming clasper lobe laterally. Clasper and manubrium roughly triangular, descending deeply into abdominal cavity; fixed process well developed; movable process variable, always with two to four heavy, pigmented, distomesad spiniform setae. Sternum IX V-shaped, proximal arm extending anterodorsally into body cavity, distal arm extending posterodorsally to form a posteroventral sheath about external genitalia, fitted distally with two free lobes armed at subapical posterior margin with modified setae. Aedeagus large, apodeme broadly scimitar shaped, bearing a weak terminal appendage. Apodemal neck present and well developed. Endchamber without well-developed, specialized lobes or with none, covered by a simple, weakly sclerotized hood, open apically and ventrally, extending from apex cephalad to a point anterior to



Figs. 10-12. Finger and clasper: 10, *A. nudatus hiemalis*; 11, *A. nudatus nudatus*; 12, *A. nudatus mexicanus*.

aedeagal struts, then curving dorsally and anteriorly as lateral lobes of aedeagal apodeme. Aedeagal pouch arising below trough, extending distally and dorsally toward base of sclerotized inner tube, latter strongly sclerotized, broad at base, ventral margin curving ventrally and cephally; narrowing to a well-developed tube posterally, apex without auxiliary sclerites. Crescent sclerite (C.S.) present. Crochets represented by very small, internal, unarticulated plates at ventral apex of endchamber. Penis rods long, coiled. Aedeagal apodemal rods present, well sclerotized. Ventral intramural rod present.

The species, though closely related, may be separated into five species groups based on characters in the male genitalia. The characters used in the grouping are: (1) number of spiniforms on finger of clasper and (2) position of spiniforms on distal or proximal portion of finger curve in either vertical or oblique rows. The grouping, though artificial, may give an indication as to the phylogeny of this genus. The five groups are:

1. Spiniforms: 1 distal, 1 proximal: *amphibolus, montanus,* and *sinuatus.*
2. Spiniforms: 2 distal, 1 proximal: *nudatus nudatus, n. mexicanus,* and *n. hiemalis.*
3. Spiniforms: 3 distal, 1 proximal: (vertical row) *martini* and *walkeri*; (oblique row) *falsicalifornicus falsicalifornicus* and *f. congruens* (*f. falsicalifornicus* has apparently lost the proximal spiniform in its evolution).
4. Spiniforms: 3 distal: *novomexicanensis, traubi, oaxacae,* and *durangoensis* (in *durangoensis* one of the distal spiniforms has apparently been lost in its evolution).
5. Spiniforms: 1 distal, 3 proximal: *nidiophilus.*

The most widely distributed group of this genus is represented by *A. amphibolus* and *A. montanus* in the north and *A. sinuatus* in the south. The northern species are most closely related to the genus *Callistopsyllus.* The *nudatus* group, represented by three subspecies, is distributed primarily on the Colorado Plateau in the Sonoran Desert, which extends into Mexico. The distribution of the *falsicalifornicus* group is coastal or subcoastal in the Pacific region of North America. The distribution of *nidiophilus, traubi,* and *oaxacae* is limited to Mexico. *Anomiopsyllus princei* has been collected only from New Mexico and *martini* only from Mexico; however, both of these species have been collected only from *Sciurus aberti,* suggesting that they could be the same species. Further collecting is needed to determine their relationship.

Key to Male *Anomiopsyllus*

1.	Finger of clasper with both distal and proximal spiniforms	2
	Finger of clasper with only distal spiniforms	11
2(1).	Finger with 1 distal and 3 proximal spiniforms	*nidiophilus*
	Finger with 1 or more distal but only 1 proximal spiniform	3
3(2).	Finger with 1 distal and 1 proximal spiniform	4
	Finger with 2 or 3 distal and 1 proximal spiniform	6
4(3).	Finger triangular shaped (Fig. 7)	*amphibolus*
	Finger boomerang shaped (Fig. 8,9)	5
5(4).	Finger broad; 3 heavy bristles on apex of St. IX (Fig. 33)	*sinuatus*
	Finger narrow; 4 heavy bristles on apex of St. IX (Fig. 32)	*montanus*
6(3).	Finger with 2 distal and 1 proximal spiniform	7
	Finger with 3 distal and 1 proximal spiniform	9
7(6).	Distance between distal spiniforms under 20u	*nudatus nudatus*
	Distance between distal spiniforms over 20u	8

8(7). Thin bristle at angle of divergence of St. IX (Fig. 35) .... *nudatus hiemalis*
Thick bristle at angle of divergence of St. IX (Fig. 36) .... *nudatus mexicanus*

9(6). Finger with distal spiniforms in oblique row in relation to posterior margin (Fig. 13) .... *falsicalifornicus congruens*
Finger with distal spiniforms in vertical row in relation to posterior margin 10

10(9). Angle of divergence of St. IX with prominent nob at angle; 1 or 2 thick bristles (Fig. 38) .... *walkeri*
Angle of divergence without nob; 2 thick bristles (Fig. 39) .... *martini*

11(1). Finger with 2 distal spiniforms (Fig. 26) .... *durangoensis*
Finger with 3 distal spiniforms (Fig. 27) 12

12(11). Finger with oblique row of spiniforms (Fig. 13) ...... *falsicalifornicus falsicalifornicus*
Finger with vertical row of spiniforms (Fig. 27) 13

13(12). Process of clasper with long bristle (Fig. 27) 14
Process of clasper without long bristle (Fig. 26) .... *novomexicanensis*

14(13). Apex of finger distinctly acuminate (Fig. 28); posterior margin of St. IX with 1 thin, submarginal bristle .... *traubi*
Apex of finger rounded (Fig. 29); posterior margin with large number of evenly spaced bristles extending from heavy apical bristles, about ¾ down the distal arm of St. IX .... *oaxacae*

Anomiopsyllus nidiophilus
Tipton and Mendez

Figs. 7, 32, 51, 67, 78, 95

Anomiopsyllus nidiophilus Tipton and Mendez, 1968, Pacific Insects 10(1): 179.182; Lewis, 1974, J. Med. Ent. 11(2): 154.

Diagnosis: Anomiopsyllus nidiophilus, though similar to *A. martini*, is the only species in the genus with one distal and three proximal spiniforms on the movable process of the clasper. Sternum VIII differs from that of all other species, except *A. sinuatus*, by having a sinus in the caudodorsal margin. The distal arm of sternum IX has a subapical constriction bearing three short, thick setae.

Female characters are not sufficiently distinctive to separate *nidiophilus* from *martini*.

Type locality: Cerro Potosi, Nuevo Leon, Mexico, 3350 m.

Type host: Nest of wood rat (probably *Neotoma albigula leucodon*).

Type specimens: Male holotype and female allotype, 38 male and 156 female paratypes, same data; 6 males and 6 females from *Neotoma albigula leucodon*, same locality as above but with dates and elevations as follows: 5 males and 2 females on 21 April 1964, 3450 m; 1 male and 2 females on 23 April 1964, 3030 m; 1 female on 11 September 1964, 3140 m; 1 female on 23 September 1964, 2990 m. Holotype and allotype in U.S. National Museum; paratypes in British Museum (Natur. Hist.), Canadian National Collection, Rocky Mountain Laboratory at Hamilton, Montana; Escuela Nacional de Cienias Biologicas (I.P.N.), Mexico, D. F.; Brigham Young University, Provo, Utah; Gorgas Memorial Laboratory, Panama; Bishop Museum and collections of R. Traub and V. J. Tipton.

Discussion: The distribution of *Neotoma albigula leucodon* is limited to the states of Coahuila, Jalisco, Mexico, Nuevo Leon, San Luis Potosi, Tamaulipas, and Zacatecas, but subspecies of *Neotoma albigula* occur in west Texas, New Mexico, Arizona, and several states in Mexico and extend northward into the southernmost areas of Colorado and Utah. Further collections are needed to define more clearly the distribution of this species in Mexico and possibly the southwestern U.S.

Anomiopsyllus amphibolus Wagner

Figs. 1-6, 30, 52, 80, 95

Anomiopsyllus nudatus Stanford, 1931 (nec Baker, 1898), Proc. Utah Acad. Sci. 8: 153 (*fide* Jellison and Good (1942: 21))

Anomiopsyllus amphibolus Wagner, 1936, Zeit für Parasitol. 8: 654-655; Jellison and Good, 1942, Index to the literature of Siphonaptera of North America: 21-24; Ewing and I. Fox, 1943, U.S. Dept. Agric. Misc. Publ. 500: 114; Stanford, 1943, Proc. Utah Acad. Sci., Arts, and Lett. 19-20: 173; Costa Lima and Hathaway, 1946, Monogr. Inst. Oswaldo Cruz 4: 127; Hubbard, 1947, Bull. S. Calif. Acad. Sci. 48(3): 116; Tipton, 1950, Great Basin Nat. 10: 63; Beck et al., 1953, Proc. Utah Acad. Sci., Arts, and Lett. 30: 50; Jellison, Locker, and Bacon, 1953, Index to the literature of Siphonaptera of North America, Suppl. 1: 10; Howell, 1957, J. Parasitol. 43(5): 40, 42; Parker and Howell, 1959, J. Parasitol. 45(6): 507-604. Stark, 1959, Siphonaptera of Utah: 105-106; Holland, 1965, Canadian Ent. 97: 1053; Beck and Allred, 1966, Brigham Young Univ. Sci. Bull., Biol. Ser. 7(2): 13; Jellison and Glesne, 1967, Index to the literature of Siphonaptera of North America, Suppl. 2: 13-19; Allred, 1968, Great Basin Nat. 28(2): 75; Tipton and Saunders, 1971, Brigham Young Univ. Sci. Bull., Biol. Ser. 15(2): 18; Lewis, 1974, J. Med. Ent. 11(2): 154.

Anomiopsylla amphibolus (sic): Howell, 1955, Great Basin Nat. 15: 40, 42; Augustson and Durham, 1961, Bull. S. Calif. Acad. Sci. 60(2): 100.

Diagnosis: Anomiopsyllus amphibolus males may be distinguished from other *Anomiopsyllus* species, except *A. montanus* and *A. sinuatus*, by having only two widely spaced spiniforms near the posterior margin of the movable process and a single row of four very strong, heavy setae on the apical posterior margin of sternum IX, and from *A. montanus* and *A. sinuatus* by the triangular-shaped movable process. The articulation of the movable process is linear and less heavily sclerotized than in *A. nudatus*. The proximal arm of sternum IX is narrower than in *nudatus* and not parallel sided, but somewhat boomerang-shaped with the hook pointed dorsad and anterad. The distal arm of sternum IX is broad basad and gradually narrows to the apex. It is more than twice as broad at the base than at the apex, with a row of 4 heavy setae followed by 6 or 7 small setae extending ventrad two-thirds of the distance up the posterior margin from the apex. The aedeagus has a distinct mid-dorsal lobe extending from a point above the aedeagal struts one-half of the distance to the apex of the endchamber.

Females are easily distinguished from other species of *Anomiopsyllus*, except *A. montanus* and *sinuatus*, by a deep sinus of sternum VII and the straight posterior margin of tergum VIII. *Anomiopsyllus amphibolus* is distinguished from *A. montanus* and *A. sinuatus* by the presence of a bulbular expansion of the terminal portion of the blind ductus seminalis (Figs. 2, 66).

Length (average): 1.2-1.8 mm.

Type locality: Salina, Sevier County, Utah.

Type host: Neotoma desertorum

Type specimens: Male holotype and female allotype, male and female paratypes collected on 21 March 1929 by J. S. Stanford, deposited in Dr. Stanford's collection at Utah State Univ., Logan, Utah.

Recorded distribution: Nevada: Beatty, Nye Co., (Hubbard, 1949); Utah: many records (Howell, Stark).

New distribution: Arizona: Mojave and Coconino counties (north of the Colorado River); Nevada: Clark and Lincoln counties.

Material examined: Arizona: Coconino Co.: 1 female, ex *Neotoma albigula*, 3 km E of Williams (juniper woodland), 20 April 1949 (PHS); 2 males, ex *Neotoma lepida*, 55-65 km N of Williams, 2134 m (cedar), 22 April 1939 (PHS). Mojave Co.: 1 male, 1 female, ex *Neotoma lepida*, 19 km NW of Hackberry, 11 m, 8 April 1939, (PHS); 1 female, ex *Neotoma lepida*, Cutler Pockets, 10 March 1957, F. E. Durham (HF); 1 male, ex *Neotoma lepida*, Mt. Trumbull, 12 March, 1957, F. E. Durham (HF); 1 female, same host, Fulton Springs, 2 April 1959, F. E. Durham (HF); 1 female, ex *Neotoma fuscipes*[5], no specific locality, 26 April 1938 (PHS). *Nevada:* Clark Co.; 1 male, 1 female, ex *Neotoma mexicana*, 16 km N, 18 km W of Las Vegas, 2592 m, 19 March 1949; 1 female, ex *Neotoma fuscipes*, no specific locality, 14 April 1938 (PHS). Lincoln Co.: 1 female, ex *Onychomys leucogas-*

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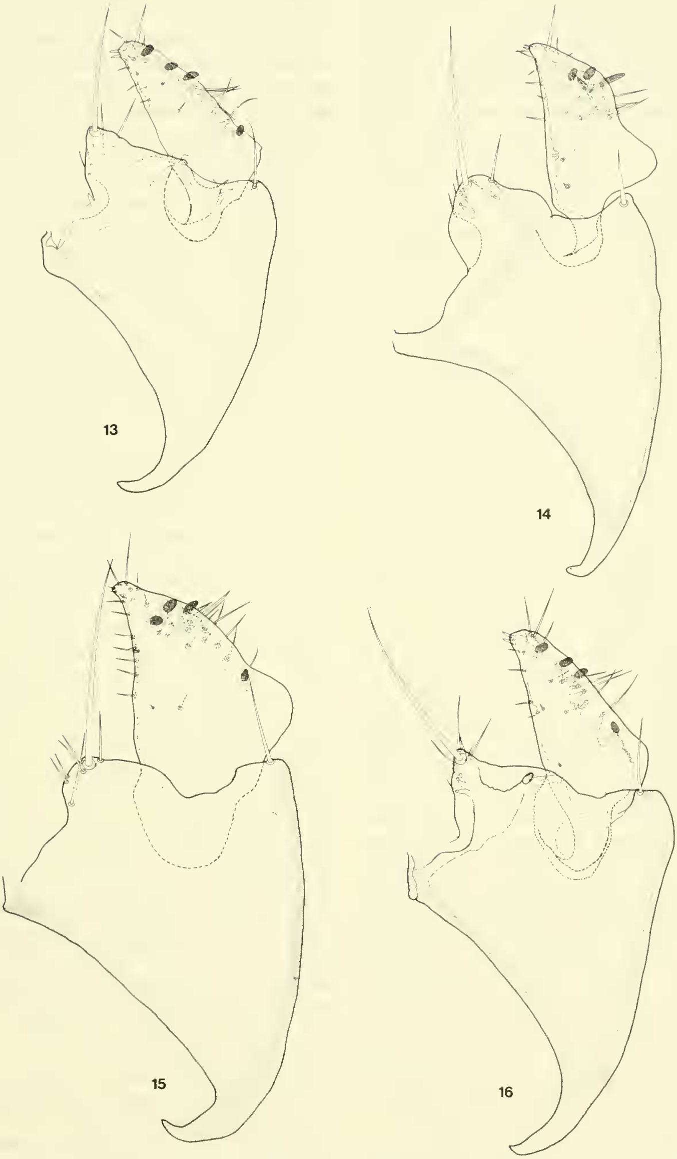
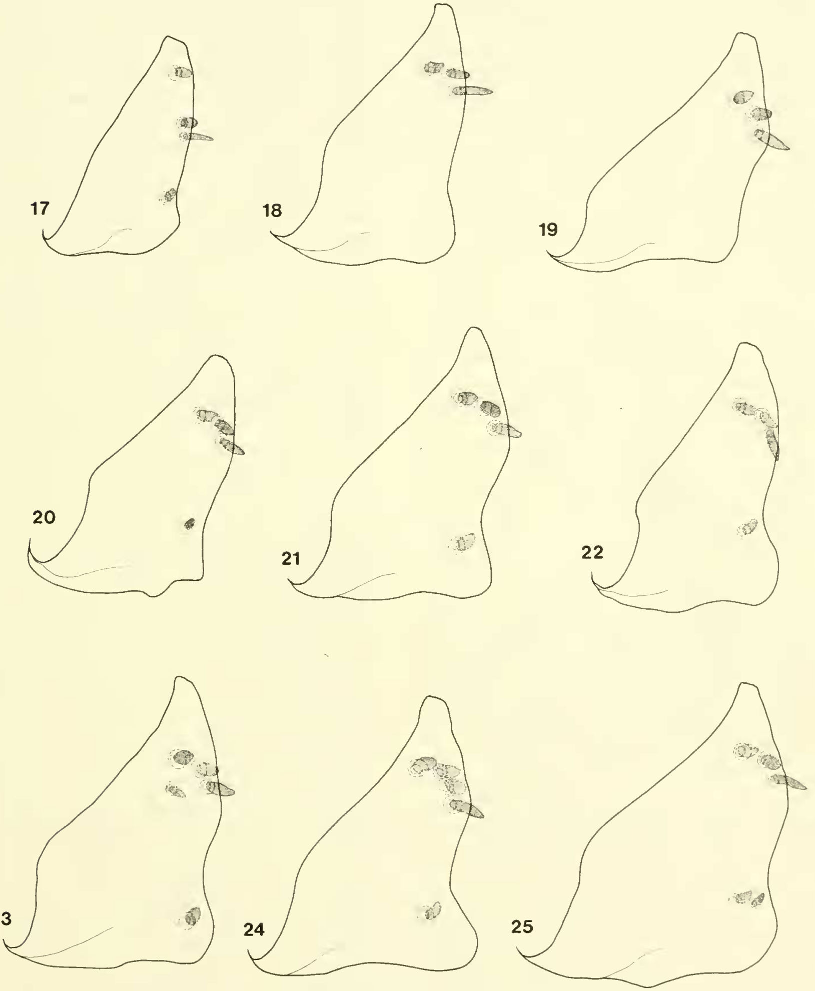
[5] The record from *Neotoma fuscipes* is undoubtedly an error, since *N. fuscipes* is not recorded from Arizona. The record should probably be ascribed to *N. albigula*.)



Figs. 13-16. Finger and clasper: 13, *A. walkeri*; 14, *A. falsicalifornicus falsicalifornicus*; 15, *A. falsicalifornicus congruens*; 16, *A. martini.*

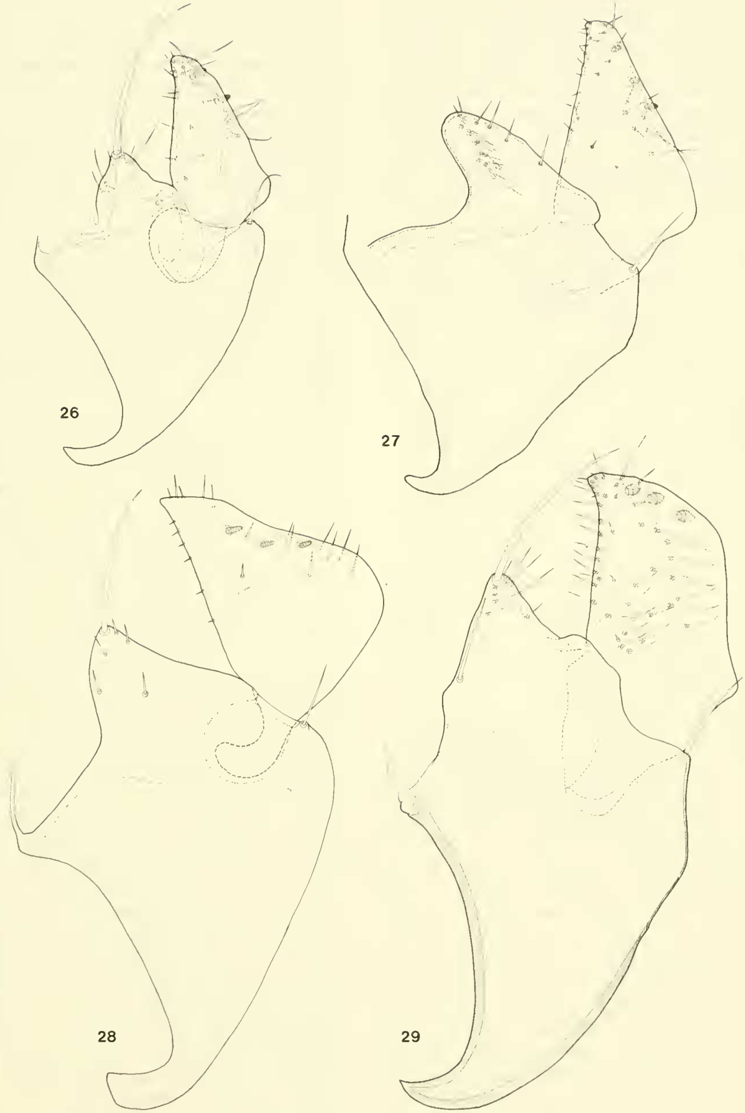
ter, 39 km SW of Caliente, 1220 m (cactus, sage), 4 May 1939 (PHS). Nye Co.: 6 males, 10 females, ex *Neotoma albigula*, 27 km NE of Pahrump, 1982 m (rocky timber), 19 December 1949, E. Kudka; 3 males, ex *Peromyscus maniculatus*, same locality, (PHS); 2 males, 4 females, ex *Neotoma lepida* nest, 28 June 1965, Merino; 1 male, ex *Neotoma lepida*, Mercury, 12 March 1961; 1 female, ex *Neotoma lepida* nest, Mercury, 15 June 1965, Merino; 1 female, same host, same location, 1 July 1965, Merino; 1 male, ex *Peromyscus*, Mercury, 6 October 1959, NAV-KAI. *Utah:* Beaver Co.: 1 female, ex *Reithrodontomys megalotis*, Wahwah Springs; 1 male, ex *Neotoma lepida*, 13-14 September 1950, D. E. Beck. Box Elder Co.: 1 male, 1 female, host not specified, Lucin small reservoir at site of abandoned CCC camp, 18 June 1952, Beck and Killpack; 2 males, 3 females, ex *Neotoma lepida*, Lucin, 14 February 1953, Beck et al. Davis Co.: 4 males, 6 females, ex *Neotoma* nest, Roy, 13 October 1951, Kohls and Sargent (RM). Duchesne Co.: 1 female, ex *Peromyscus maniculatus*, locality not stated (Bluebell, junipers), 21 March 1953, Killpack. Grand Co.: 1 male, ex *Neotoma* sp., Devil's Garden Area of Arches National Monument, 10 May 1950, D. M. Allred; 6 males, 6 females, ex *Neotoma lepida* nest, Moab S side of U 93 near willow sweeps 4.8 km W of Arches National Monument (red sandstone), 1 September 1950, D. M. Allred; 4 males, 4 females, same host, Moab 1.6 km S of US 160 and U 93 Junction (Navajo sandstone environs), 9 September 1950, D. M. Allred; 9 males, 20 females, same host, .8 km S of US 160 and U 93 Junction (Navajo sandstone environs), 9 September 1950, D. M. Allred. Iron Co.: 2 females, ex *Neotoma lepida* nest, 14.5 km W of Parowan (canyon defile), 6 September 1950, Beck and Allred. Juab Co.: 1 male, ex *Neotoma lepida*, 1.6 km NW of Joy, 1 June 1951, Allred et al.; 4 males, 10 females, same host, Fish Springs mine shaft in foothills 4.8 km N of Harris Ranch House (rocky ledges), 15 June 1951, Beck et al.; 3 males, 8 females, ex *Neotoma Lepida* nest, Lynndyl (fallen tree, consisting of juniper twigs and bark), 17 November 1951, Barnum and Moore; 30 males, 40 females, ex *Neotoma lepida*, N of Lynndyl and E of old CCC camp, same date, Barnum and Moore; 2 males, 1 female, same host, Lynndyl (juniper tree), same date, Barnum and Moore; 40 males, 39 females, ex *Neotoma lepida* nest, N of Lynndyl and E of CCC camp, 17 November 1951, Milander and Cloward; 151 males, 169 females, same host, E of Jericho (juniper), 13 December 1952, Beck et al.; 136 males, 165 females, same host, Jericho by US 6, 13 March 1954, Howell and Beck; 35 males, 74 females, same host, Jericho E side of Hwy 50-6, 4.5 km N of train station (cedar), 11 April 1954, J. F. Howell; 23 males, 49 females, same host, same location, 8 May 1954. J. F. Howell; 1 male, 8 females, same host, N of Jericho on E side of Hwy 50-6, 9 June 1954, J. F. Howell; 2 males, 2 females, same host 4.5 km N of Jericho (juniper and sage), 8 July 1954, J. F. Howell; 1 female, same host, Jericho (juniper and sage), 21 July 1954, Howell and Beck; 2 males, same host, 4.8 km N of Jericho, 3 September 1954, J. F. Howell; 1 male, 4 females, ex *Neotoma lepida lepida* nest, 4.8 km N of Jericho on US 6, 29 September 1954, J. F. Howell; 41 males, 68 females, same host, same location, 8 October 1954, J. F. Howell; 81 males, 82 females, ex *Neotoma lepida* nest, Jericho E side of US 6, 4.5 km N of train station, 6 February 1954, Howell and Beck; 18 males, 39 females, ex *Neotoma lepida*, 4.8 km N of Jericho on E side of US 6, 29 October 1954, Howell and Jaussi; 65 males, 65 females, same host, same location, 12 November 1954, Howell; 207 males, 285 females, ex *Neotoma lepida*, same location, 2 December 1954, Howell and Nielson; 40 males, 39 females, ex *Neotoma lepida* nest, 4.8 km NE Jericho, 7 January 1954, J. F. Howell; 75 males, 69 females, same host, 4.8 km NE of Jericho on E side of US 6, 25 January 1955, J. F. Howell; 12 males, 8 females, ex *Neotoma lepida*, 4.8 km NE of Jericho, 3 March 1959, BYU. Kane Co.: 1 male, ex *Dipodomys ordii*, 16 February 1972, NAV-KAI; 24 males, 7 females, ex *Neotoma albigula*, 5 December 1971, NAV-KAI; 1 female, ex *Neotoma lepida*, Navajo Wells, 24 June 1951, BYU; 1 male, 1 female, same host, 8.8

km W of Adairville in Catstaire Canyon (rocky area), 8 September 1951, Beck and Allred; 1 female, same host, Navajo Wells SW of Corral (rocky ledges), 7 September 1951, Beck and Allred; 1 male, 1 female, same host, same location, 6 September 1951, Beck and Allred; 1 male, 1 female, same host, W entrance to Catstaire Canyon (Upper Sonoran sagebrush), 9 May 1952, M. D. Coffey; 1 male, 2 females, ex *Neotoma lepida* nest, Catstaire Canyon (sagebrush), 8 May 1952, M. D. Coffey; 1 male, same host, W entrance to Catstaire Canyon (rocky ledge), same date, M. D. Coffey; 8



Figs. 17-25. Variations in spiniform placement on finger: 17, *A. nudatus mexicanus*; 18-25, *A. falsicalifornicus congruens*.

males, 9 females, ex *Peromyscus crinitus*, 11 December 1971, NAV-KAI; 1 male, 2 females, ex *Peromyscus maniculatus*, 40.2 km E of Kanab about 457 m off road near Paria and King manganese mine roads junction, 9 May 1952, M. D. Coffey; 1 male, 1 female, ex. *Peromyscus truei*, 17 February 1972, NAV-KAI. 4 males, 2 females, ex *Neotoma cinerea*, 6.4 km N of Kanab, 1494 m, 14 April 1949 (PHS). Millard Co.: 11 males, 31 females, ex *Neotoma lepida*, Lynndyl, 17 November 1951, Melander and Cloward. San Juan Co.: 1 female, ex *Neotoma albigula*, Montezuma Creek 4.8 km N of trading post, Beck et al.; 1 male, 6 females, ex *Neotoma mexicana*, Blanding, 7 September 1956; 1 male, 1 female, ex *Peromyscus maniculatus* 32.2 km S of Moab (sandy wash cliff), 7 May 1951, Allred et al.; 3 males, 2 females, ex *Neotoma lepida*, Yuba Dam 1.6 km from Hwy 28, 182.8 m W on N side of reservoir, 18 April 1952, Beck and Beck; 9 males, 9 females, ex *Neotoma lepida* nest, Yuba Dam, 29 April 1960, Beck. Sanpete Co.: 2 males, 2 females, ex *Neotoma lepida*, Yuba Dam, 18 April 1952, D. E. Beck. Tooele Co.: 1 female, ex *Neotoma lepida* 3.2 km N Little Granite Mt., 10 March 1955, E. A. Shippee (U of U); 1 male, 1 female, ex *Neotoma* sp. nest, Sandy Pars, Dugway Valley, 15 April 1954, D. Allred (U of U); 3 males, 1 female, ex *Neotoma lepida* nest, Dugway Proving Grounds, 3 March 1955 (U of U); 10 males, 7 females, same host, same location, 14 April 1955 (U of U); 1 male, 1 female, same host, same location, 6 April 1955 (U of U); 17 females, same host, same location, 6 January 1955 (U of U); 13 males, 12 females, same host, same location, 7 February 1955 (U of U); 1 male, 1 female, same host, same location, 20 January 1955 (U of U); 10 males, 12 females, same host, same location, 20 January 1955 (U of U); 10 males, 12 females, same host, same location, 16 March 1955 (U of U); 3 males, 2 females, same host, same location, 9 December 1954 (U of U); 6 females, same host, same location, 27 October 1954 (U of U); 6 males, 1 female, same host, same location, 24 November 1954 (U of U); 1 female, ex *Peromyscus truei*, Cane Springs, Cedar Mts., Dugway Proving Grounds, 21 January 1953 (U of U); 1 male, ex *Peromyscus crinitus*, Camel Back Mt., Dugway Proving Grounds, 30 January 1953 (U of U). Uintah Co.: 1 male, ex *Peromyscus maniculatus*, Dinosaur National Monument 1.2 km SSW of headquarters on N bank of river (sandy wash), 14 August 1951, Beck et al. Utah Co.: 8 males, 14 females, ex *Neotoma*, Chimney Rock Pass, 25 October 1968, Clark; 1 female, ex *Neotoma* nest, Provo, top of ladder in Buckley's mine in Rock Canyon, 24 November 1948, D. M. Allred; 1 female, ex *Neotoma cinerea*, Springville, 29 November 1948, V. J. Tipton; 2 males, ex *Neotoma cinerea* nest, Thistle (tunnel composed of rags, sticks, paper, plants, rope, and many bones), 2 November 1951, Barnum et al.; 10 males, 16 females, same host, Spanish Fork Canyon, 2 November 1951, Barnum et al.; 3 males, 1 female, same host, Spanish Fork Canyon, cave N of Ma's and Pa's Cafe in Canyon, 5 November 1951, Barnum et al.; 1 female, 2 males, ex *Neotoma lepida*, Eureka, 17 November 1951, Barnum and Moore (BYU); 1 female, ex *Neotoma cinerea*, Spanish Fork Canyon, small cave (dried plants), 2 November 1951, W. Milander; 1 female, ex *Neotoma lepida*, Elberta, Chimney Rock Pass, 15 October 1949, D. M. Allred; 19 males, 29 females, ex *Neotoma lepida* nest, Cedar Valley (juniper-rocky hillside), 22 February 1953, Beck and Coffey; 1 female, ex *Neotoma lepida*, nest, NE Chimney Rock Pass near abandoned mine, 28 March 1953, Coffey and Liddiard; 1 female, ex *Peromyscus maniculatus*, Cedar Valley on hill NE of big juniper grove, 25 March 1951, Allred et al.; 1 male, 2 females, same host, 3.2 km W of Genola on main Hwy to Eureka (rocky cliffs), 13 January 1952, D.E. Beck. Washington Co.: 1 female, ex *Neotoma lepida*, Beaver Dam Mtns., 22 April 1953, Howell; 1 male, ex *Dipodomys merriami*, W side Beaver Dam Wash bottom (alfalfa fields of Terry Ranch), 21 December 1950, Beck and Allred; 1 female, ex *Dipodomys merriami*, 3.2 km S of Rockville, 13 July 1953, Beck and Killpack; 1 female, ex *Neotoma lepida*, St. George, 25 November 1949, Allred and Barnum; 43 males, 63 females, ex *Neotoma lepida* nest, Beaver Dam Wash, .8 km NE



Figs. 26-29. Finger and clasper: 26, *A. durangoensis*; 27, *A. novomexicanensis*; 28, *A. traubi* (redrawn fom Barrera 1951 and Barnes 1963); 29, *A. oaxacae*.

Terry Ranch (joshua tree peat), 21 December 1950, Beck and Allred; 2 males, 5 females, same host, Beaver Dam Wash of Beaver Mtns. (joshua tree foothills), 23 February 1952, D. E. Beck; 1 female, ex *Neotoma lepida*, Beaver Dam Wash (flat, gravel), 16 April 1952, Grant et al.; 1 female, ex *Peromyscus eremicus*, S of Hwy 15 and Berry Springs (sandy area), 19 December 1950, Beck and Allred; 1 female, same host, Berry Springs (lava rock), 19 December 1950, Beck and Allred; 1 female, ex *Peromyscus maniculatus*, 6.4 km W of Hwy 59 state line crossing at Utah-Arizona border, 12 July 1952, Beck and Killpack; 4 females, ex *Neotoma lepida* nest, Rush Valley (juniper), 9 November 1951, Barnum et al.; 2 females, ex *Neotoma lepida* nest, Toquerville, 5 September 1951, Beck and Allred. *Wyoming:* Sweetwater Co.: 1 female, ex *Neotoma cinerea*, 24 km SW of Green River, 1920 m (rocky ledges), 23 August 1938 (PHS).

Discussion: This species is most closely related to *A. montanus*. Characteristics of the male clasper, e.g., configuration of the fixed process of the clasper and presence of a row of setae above the acetabular seta (Fig. 6), show relationship between males of these two species. The shape of the spermatheca and configuration of sternum VII (Fig. 80) indicate a relationship between the females of these two species.

With the exception of *A. montanus*, *amphibolus* occurs farther north than any other species of *Anomiopsyllus*, and it is the Great Basin representative of the genus. The distributional pattern includes northwestern Arizona from whence it extends northward between the Rocky Mountains and the Sierra Nevada Mountains into Wyoming. The species has been recorded most frequently from Utah where much research has been conducted by Allred, Beck, Howell, and Tipton at Brigham Young University and Stanford at Utah State University. This species has also been recorded from Nye and Douglas counties, Nevada (Beck et al. 1953, Hopkins and Rothschild 1962). Its distribution may include those parts of eastern and northeastern California which have a habitat similar to that of the Great Basin and where *Neotoma lepida* occurs, but we have not collected *A. amphibolus* from that area during this study.

The primary host appears to be *Neotoma lepida*, although records include *N. cinerea* and *Peromyscus* in frequent numbers. Records from fortuitous hosts are most often obtained during plague surveys.

Stark (1959) has pointed out that *A. amphibolus* may prefer dry habits, since nests of *N. cinerea* occurring at high elevations (noted in Beck et al. 1953) had fewer fleas per nest than those of *N. lepida* occurring at lower elevations. This fails to take into consideration possible host differences, which may be a significant factor. *Neotoma cinerea* has been placed in a separate subgenus by Goldman (1910), Hall and Kelson (1959), and others, and may well differ significantly from the standpoint of flea host selection.

Howell (1957) states that in the vicinity of Jericho, Juab County, Utah, *A. amphibolus* adults appear in nests of *N. lepida* in October and reach a peak in December. This seasonal distribution almost duplicates that of *A. falsicalifornicus* in California.

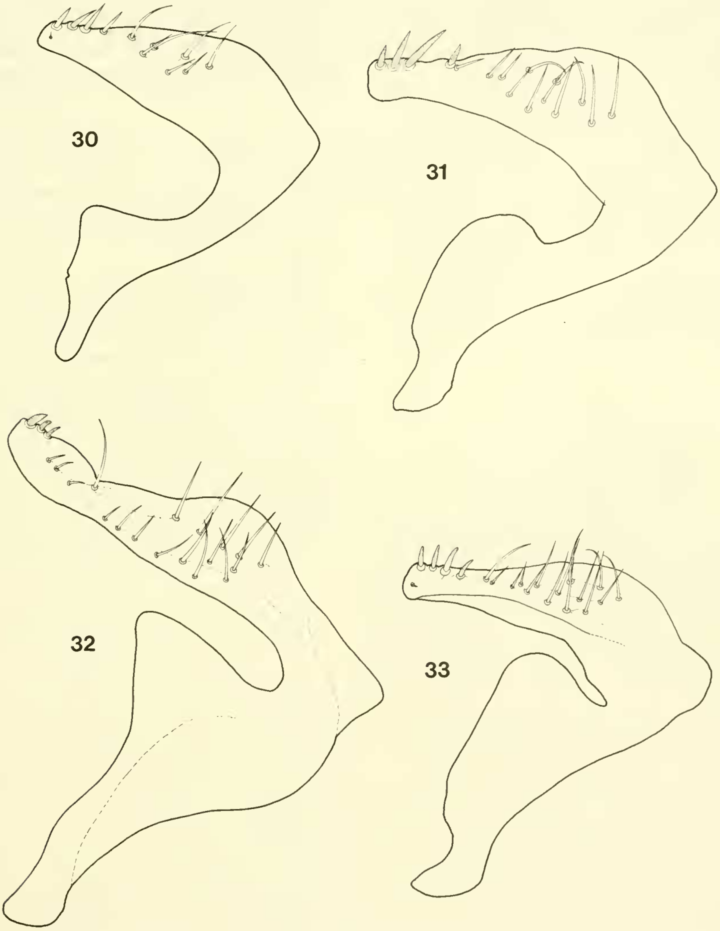
Among the many specimens examined, very little variation was evident; *A. amphibolus* from northwestern Arizona did not differ in any significant detail from specimens collected in Utah. This is in distinct contrast to some *Anomiopsyllus* species, e.g. *A. falsicalifornicus*, which shows considerable variation both geographically and among individuals in a series. The apparent stability of *A. amphibolus* over a broad area may be explained in part by the rather continuous distribution of its host, *N. lepida*, through the Great Basin (see Hall 1946). The climate of the Great Basin, though complex, changes primarily with latitude and altitude. Populations of *A. amphibolus* would be expected to be relatively continuous with much opportunity for uninterrupted gene flow. The area occupied by *A. falsicalifornicus* is subject to more climatic variability resulting not only from very heterogeneous topography and latitude, but also from proximity to or distance from the sea. Populations of *A. falsicalifornicus* are disjunct in their distribution (of both the total population and especially the local populations) which results in much gene flow interruption.

Anomiopsyllus sinuatus Holland

Figs. 9, 33, 54, 65, 79, 94

Anomiopsyllus sinuatus Holland, 1965, Canadian Ent. 97: 1053, 1058; Lewis, 1974, J. Med. Ent. 11(2): 154.

Diagnosis: Anomiopsyllus sinuatus is closely related to *A. montanus* in that both have the movable process L-shaped with a large, blunt spiniform mesally inserted at the distal and proximal portions. *Anomiopsyllus sinuatus* has a broader, shorter process than *montanus*. The ninth sternum differs from that of *A. montanus* by the presence of three thickened setae followed by a row of thinner setae as compared to four thick setae in *A. montanus*. The sinus formed by the inner margins of the proximal and distal arms is deep and narrow in



Figs. 30-33. Male ninth sternum: 30, *A. amphibolus*; 31, *A. montanus*; 32, *A. nidiophilus*; 33, *A. sinuatus*.

sinuatus and broadly rounded in *montanus*. *Anomiopsyllus sinuatus*, like *A. montanus*, has a sinus on the caudal border of sternum VIII.

Female characters are not sufficiently distinctive to separate *sinuatus* from *montanus*.

Type locality: 48 km W of Durango, Durango, Mexico, 1982 m.

Type host: Nest of *Peromyscus* sp.

Type specimens: Male holotype and female allotype, 4 male and 11 female paratypes collected on 5 June 1961 by J. E. H. Martin, deposited in the Canadian National Collection.

Discussion: Anomiopsyllus sinuatus and *A. montanus* present an interesting distributional problem in that *montanus* has only been collected at the northern distribution of *Anomiopsyllus* and *sinuatus* has only been collected at the southern portion. Collections so far have not indicated that there are any intermediate forms between these two populations; however, further specimens should be collected with the view of linking these geographically separated species.

Anomiopsyllus montanus Collins

Figs. 8, 31, 53, 66, 81, 94

Anomiopsyllus montanus Collins, 1936, Ent. News 47: 128-130; Ewing and I. Fox, 1943, U.S. Dept. Agric. Misc. Publ. 500: 115; Hubbard, 1947, Fleas of western North America: 82-83; Holland, 1952, Canadian Ent. 84(3): 65-72; Holland, 1965, Canadian Ent. 97: 1053, 1055, 1058; Senger, 1966, J. Kans. Ent. Soc. 39(1): 106; Jellison and Glesne, 1967, Index to the literature of Siphonaptera of North America, Suppl. 2: 13-19; Jellison and Senger, 1973, Mont. Agr. Exp. Sta. Res. Rept. 29: 18-19; Lewis 1974, J. Med. Ent. 11(2): 154.

Arctopsylla montanus: Jellison, Kohls, and Mills, 1943, Mont. State Board Ent. 2: 2 (error for *Anomiopsyllus*).

Anomiopsyllus nudatus: Dunn and Parker, 1923, Public Hlth. Rept. 38: 2774-2775 (misidentification).

Diagnosis: Anomiopsyllus montanus is closely related to *A. sinuatus* but differs in that there are four heavy setae near the apex of sternum IX instead of three as in *sinuatus*. The movable process of *A. montanus* is narrower and longer with a deeper sinus than in *sinuatus*.

Female characters are not sufficiently distinctive to separate *montanus* from *sinuatus*.

Type locality: Canyon Creek, W of Hamilton, Montana.

Type host: Bubo virginianus occidentalis

Type specimens: Male holotype and female allotype collected in 1922 by L. H. Dunn and R. R. Parker, deposited in the National Institutes of Health.

Discussion: This flea was first collected from a horned owl (*Bubo virginianus*) near Hamilton, Montana, and identified as *Anomiopsyllus nudatus* by Dunn and Parker (1923). Collins (1936) rectified the misdetermination and described the species as new.

Subsequent records have been few. We have examined only material from near Hamilton, Montana, from *Bubo virginianus* (part of the original series) and *Neotoma cinerea*. Holland (1952) recorded the species from near Banff, Alberta, Canada. No other records are available.

Anomiopsyllus montanus has the northernmost distribution of any species in the genus. We suspect that the primary host is a species of *Neotoma*, possibly *N. cinerea* since no other *Neotoma* species occurs as far north as Hamilton, Montana, and Alberta, Canada (Hall and Kelson 1959). The original discovery of this flea on the horned owl should not be considered too unusual, as fleas are often found on the predators of their hosts. In addition, horned owls often nest in cliffs, which are a preferred nesting site of *N. cinerea*.

Anomiopsyllus nudatus nudatus (Baker)

Figs. 11, 36, 55, 68, 84, 94

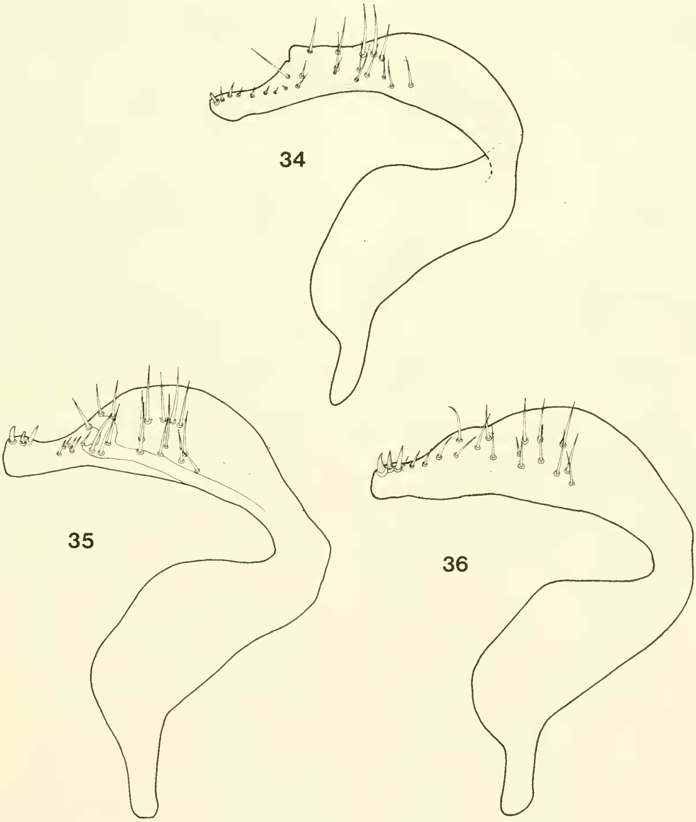
Typhlopsylla nudata Baker, 1898, J. N. Y. Ent. Soc. 6: 56.

Anomiopsyllus nudatus Baker, 1904, Proc. U.S. Nat. Mus. 27: 425, 426, 452; Fox, 1914, Hyg. Lab. Bull. 97: 25; Jordan and Rothschild, 1915, Ectoparasites 1: 45; Dunn and Parker, 1923, Public Hlth. Repts. 38: 2774-2775; Fox, 1929, Ent. News 40: 218; Hirst, 1926, Ceylon J. Sci. 1: 261; Wagner, 1930, Mag. de Parasitol. 1: 135; Stanford, 1931, Proc. Utah Acad. Sci. 1931: 153; Collins, 1936, Ent. News 47: 129-130; Eskey and Haas, 1939, Public Hlth. Repts. 54: 1472; Eskey and Haas, 1940, Public Hlth. Bull. 254: 29-74; Hubbard, 1940, Pac. Univ. Bull. 37(4); Augustson, 1943, Bull. South. Calif. Acad. Sci. 42(2): 73; Ewing and I.

Fox, 1943, U.S. Dept. Agric. Misc. Publ. 500: 115; Hubbard, 1947, Fleas of western North America: 79-80; Eads and Menzies, 1948, J. Kans. Ent. Soc. 21: 135; Hubbard, 1949, Bull. South. Calif. Acad. Sci. 48: 125; Pollitzer, 1952, Bull. WHO 7: 231-342, Annex 1; Augustson and Wood, 1953, Bull. South. Calif. Acad. Sci. 52: 48-56; Wehrle, 1953, Pan-Pacific Ent. 24: 39; Holdenreid and Morlan, 1955, J. Inf. Dis. 96: 135; Augustson, 1955, Bull. South. Calif. Acad. Sci. 54(1): 36-39; Knudsen, 1956, Bull. South. Calif. Acad. Sci., 55(1): 1-63; Beer et al., 1959, J. Parasitol. 45(6): 605-623; Stark, 1959, Siphonaptera of Utah: 107; Holland, 1965, Canadian Ent. 97: 1051-1058; Barnes, 1965, Pan-Pacific Ent. 41(4): 272-280; Jellison and Glesne, 1967, Index to the literature of Siphonaptera of North America, Suppl. 2: 13-19; Tipton and Saunders, 1971; Brigham Young Univ. Sci. Bull., Biol. Ser. 15(2): 18; Pratt and Stark, 1973, DHEW Publ. 74-8267: 11; Haas et al., 1973, J. Med. Ent. 10(3): 282; Lewis, 1974, J. Med. Ent. 11(2): 154.

Anomiopsyllus californicus: Baker, 1904, Invert. Pac. 1: 39-40; Fox, 1926, Pan-Pacific Ent. 2: 183-184.

Diagnosis: The three subspecies of *A. nudatus: nudatus, mexicanus,* and *hiemalis* can only be distinguished from each other by characters in the males. This separation is based on characters of the movable process and sternum IX. *Anomiopsyllus nudatus nudatus* can be separated readily from the other two subspecies by the presence of two closely spaced (less than 20 u) spiniforms on the distal portion of the movable process and the presence of a thin bristle at the arc



Figs. 34-36. Male ninth sternum: 34, *A. nudatus hiemalis*; 35, *A. nudatus mexicanus*; 36, *A. nudatus nudatus.*

of curvature of the distal arm of sternum IX. The movable process of the clasper in *nudatus nudatus* is narrow (M = 68 u, range 58 to 74 u) at base measured at the widest point and relatively short (M = 109 u, range 102 to 119 u).

Female characters are not sufficiently distinctive to separate the subspecies of *nudatus*.

Length: (average)—Male, 1.2 mm; female, 1.8 mm.

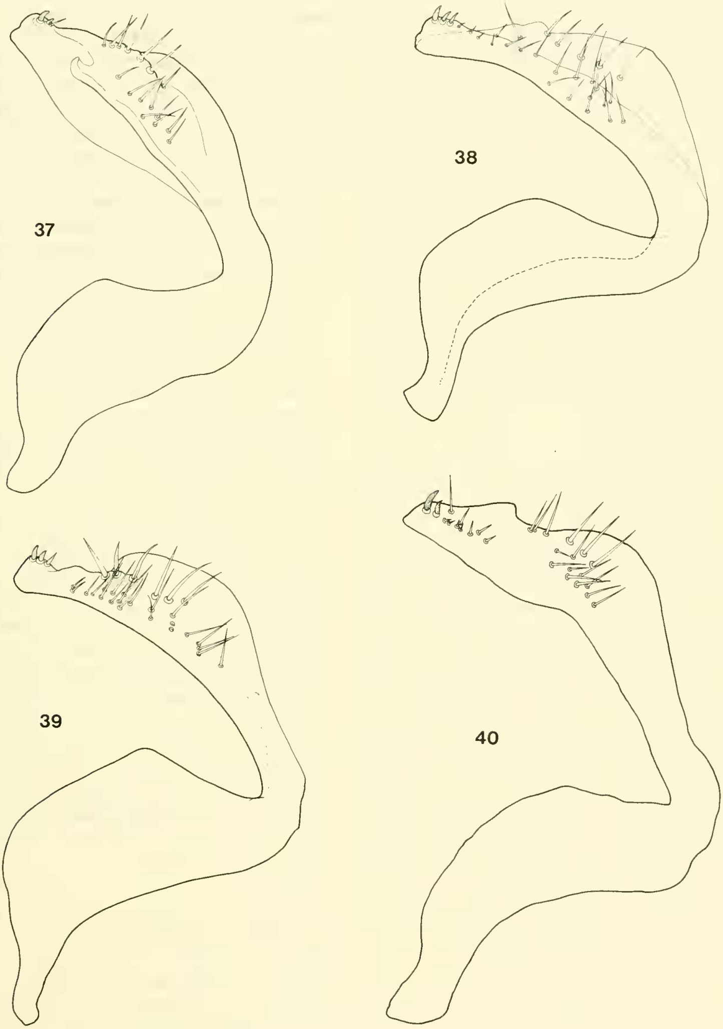
Type locality: Tucson, Pima Co., Arizona.

Type host: Neotoma albigula.

Type specimen: Female, U.S. National Museum.

Material examined: Arizona: Cochise Co.: 1 male, ex *Neotoma lepida*, 29 October 1938 (PHS); 1 male, ex *Neotoma lepida*, no date (PHS). Pima Co.: 1 female, ex *Neotoma lepida*, 7 February 1939 (PHS); 1 female, ex *Neotoma lepida*, 3 November 1938 (PHS); 1 female, ex *Neotoma lepida*, 4 November 1938 (PHS); 1 female, ex *Dipodomys merriami*, 7 February, 1939 (PHS); 1 male, ex *Spermophilus harrissi*, 8 February 1939 (PHS). *California:* Kern Co.: 1 male, ex *Neotoma* sp. Burbank Girl Scout Camp, Frazier Mtn. (oak, pine), 2 June 1958, Campbell (BVC); 1 female, ex *Neotoma fuscipes* nest, 0.8 km E of Frazier Park (oak woodland), 1 April 1959, Barnes (BVC); 17 males, 37 females, ex *Neotoma fuscipes* nests, 6.9 km N, 3.7 km W of Willow Springs (juniper woodland), 19 February 1959; 25 males, 54 females, same host, same locality, 22 January 1960. Los Angeles Co.: 13 males, 34 females, ex *Neotoma fuscipes* nests, 7.7 km N, 3 km W of Sandburg (oak woodland), 1 April 1959, Barnes (BVC); 10 males, 28 females, ex *Neotoma fuscipes* nests, 4.5 km S, 1477 km W of Fairmount (juniper woodland), 1 April 1959, Barnes (BVC); 8 males, 17 females, ex *Neotoma fuscipes*, 2.2 km S of Gorman (oak, yucca), 1 April 1959, Barnes (BVC); 1 male, 1 female, ex *Neotoma fuscipes*, School Canyon 5.9 km E of Glendale (oak woodland), 28 January 1959, D. Rohe (BVC); 1 male, 1 female, ex *Neotoma fuscipes*, Burbank (oak woodland), 6 April 1959, D. Rohe (BVC); 3 males, 2 females, ex *Neotoma lepida*, Big Tujunga Canyon, 4 January 1942, J. Couffer (HF); 1 male, 3 females, ex *Neotoma lepida*, San Gabriel Canyon, 15 January 1942, G. Augustson (HF); 3 males, 1 female, ex *Neotoma* nest, Chilao, 16 August 1942, G. Augustson (HF). Orange Co.: 1 female, ex *Neotoma* sp., Irvine (cactus, *Nicotiana*), 19 April 1955, J. Poll (BVC); 1 male, 1 female, ex *Neotoma* sp., same locality (cactus, *Nicotiana*), 26 March 1957, E. Perry (BVC); 5 males, 6 females, ex *Neotoma* sp., same locality (cactus, *Nicotiana*), 19 November 1952, J. Poll (BVC); 12 males, 20 females, ex *Neotoma fuscipes* nest, Santiago Canyon (cactus, *Nicotiana*), no date, G. Augustson (HF). Riverside Co.: hundreds, ex *Neotoma fuscipes*, San Timoteo, many dates, R. Ryckman; 3 females, ex *Neotoma* sp., 1.6 km E of McAfee Ranch, San Timoteo Canyon, 18 March 1955, J. Poll (BVC); 6 females, ex *Neotoma* nest, Matthew Lake, 3 February 1951, Ames; 4 females, ex *Neotoma lepida*, Matthew Lake, 3 February 1951, Ames; 2 males, 9 females, ex *Neotoma lepida*, Matthew Lake, 8 February 1951, Ames. San Bernardino Co.: 2 males, 1 female, ex *Neotoma lepida*, San Bernardino (oak woodland and chaparral), 21 March 1957, Barnes (BVC); 1 female, ex *Neotoma lepida*, 5.4 km N, 6.4 km E of Pioneer Town (joshua tree, yucca), 3 December 1956, K. Murray (BVC); 8 males, 3 females, ex *Neotoma lepida*, 3.2 km to 3.8 km NW of Yucca Valley (yucca desert), 4 December 1956, K. Murray (BVC); 68 males, 144 females, ex *Neotoma fuscipes* nest, 1.6 km E of Cajon (heavy chaparral), 22 December 1957, Barnes (BVC); 1 male, 1 female, ex *Neotoma fuscipes* nest, 3.5 km SE of Desert Springs (juniper woodland), 22 January 1959, Barnes (BVC); 1 female, ex *Neotoma* sp., George Air Force Base, Victorville (juniper woodland), 25 October 1951, J. Poll (BVC); 1 male, 2 females, ex *Neotoma* sp., Big Bear Lake (oak, pine), 30 May 1951, J. Poll (BVC); 1 female, ex *Neotoma* sp., Seven Oaks, 10 May 1936 (RM); 1 male, 8 May 1936 (RM); 1 female, ex *Neotoma lepida*, Batista Canyon, 28 February 1951, Ames. San Diego Co.: 5 males, 9 females, ex *Neotoma fuscipes* nests, 3 km E of Banner (juniper, *Rhus ovata* woodland), 23 March 1960, Barnes (BVC); 10 males, 9 females, ex *Neo-*

toma fuscipes nest, 16 km E of Ramona (oak woodland), 23 March 1960, Barnes (BVC); 65 males, 122 females, ex *Neotoma fuscipes* nest, Alvarado Canyon, San Diego (oak wood and chaparral), 21 March 1960, Barnes (BVC); 1 male, ex *Neotoma fuscipes* nest, 7 km S of Julian, 1219 m (oak woodland), 22 March 1960, Barnes (BVC); 4 males, 1 female, ex *Neotoma* nest, 3 km W of Guatay (oak woodland), 2 September



Figs. 37-40. Male ninth sternum: 37, *A. falsicalifornicus falsicalifornicus*; 38, *A. walkeri*; 39, *A. martini*; 40, *A. falsicalifornicus congruens*.

1955, H. Stark (PHS); 1 female, ex *Neotoma* sp., San Diego, 1936, Eskey (PHS). Ventura Co.: 2 males, 7 females, ex *Neotoma fuscipes* nests, Alder Creek 987 km N, 2.9 km W Fillmore, 28 January 1960, Barnes (BVC); 1 male, 1 female, ex *Neotoma* sp., Ozena Public Camp 2.5 km E of Hwy. 399, 26 March 1957, J. Poll (BVC); 1 male, ex *Neotoma* sp., Sycamore Canyon, 29 June 1955, E. Perry (BVC). *Nevada:* Nye Co.: 1 male, ex *Neotoma lepida*, Beatty, no date. *Utah:* San Juan Co.: 1 male, ex *Peromyscus maniculatus*, 32 km S of Moab, 8 May 1951, (Tipton and Allred); 1 male, 2 females, ex *Neotoma albigula*, Recapture Canyon, 1738 m, 16 August 1939 (PHS); 1 male, 1 female, ex *Neotoma mexicana*, Westwater Canyon, 3.2 km S of Blanding, 1830 m, 19 August 1939 (PHS).

New distribution: Arizona: Cochise Co. (PHS); *California:* Kern Co. (BVC), Riverside Co. (BVC, Ryckman), San Bernardino Co. (BVC), San Diego Co. (BVC and PHS), Ventura Co. (BVC).

Discussion: C. F. Baker (1898) described *A. nudatus* on the basis of "... two females collected by Mr. Hubbard from the inner nest of *Neotoma albigula* at Tucson, Arizona," placing the species in the genus *Typhlopsylla*, pending better knowledge of its relationships. Later, Baker (1904) described the species further and created the new genus *Anomiopsyllus* to contain it and the concurrently described *A. californicus* from Claremont, Los Angeles County, California (based on a series of females).

Baker, at the time of the original description of *nudatus*, did not designate either of his two female specimens as types, but both were deposited in the U.S. National Museum. Since both specimens were collected in the Sonoran Desert at Tucson, Arizona, the subspecies occupying that area becomes the nominate subspecies. Jordan and Rothschild's male allotype, unfortunately, falls into another subspecies occupying the Colorado Plateau from eastern Arizona through New Mexico. Though their specimen was not available for study, the figure in the original description (Jordan and Rothschild 1915) is quite clearly that of the *A. n. mexicanus*. The same figure is reproduced in Hopkins and Rothschild (1962). Nevertheless, their specimen is the first described male for the genus and for the species.

Jordan and Rothschild (1915) examined Baker's types and declared *californicus* a synonym of *nudatus* on the basis of similarities in the spermathecae and in characters of the metatarsal setae. Jordan and Rothschild described and figured a male of *nudatus* from Paradise, Arizona, designating their specimen as allotype. Although their specimen is of *nudatus*, the "allotypic" locality falls within the range of *A. n. mexicanus*. Their figure of the movable process is clearly that of *mexicanus*.

Carroll Fox (1926) acquired a series of *Anomiopsyllus* from Claremont, California, the type locality of *californicus*, which included a male differing from that described as *nudatus* by Jordan and Rothschild. He, therefore, concluded the latter authors to be in error concerning the synonomy, and described the new male as allotype of Baker's revived *A. californicus*. Jordan, on examining Fox's series, found two species; one "true *californicus*" identical to Baker's types, the other a new species requiring a name (Fox 1929). Fox (1929), therefore, named the species *A. falsicalifornicus*, based on his 1926 description. Collins (1936), in separating *A. montanus* from *nudatus*, agreed with Jordan and Rothschild's synonomy and figured the female sternum VII of both *nudatus* and *falsicalifornicus*.

Neither the characters used by Baker nor those used by Jordan and Rothschild (1915) are tenable. No character involving tarsal setation or shape of spermatheca has been found reliable in this study. Nevertheless, sternum VII of females offers some degree of reliability which, together with distributional evidence, confirms Jordan and Rothschild's synonomy.

As treated here, *A. nudatus* includes three subspecies, differentiated on the basis of male morphological characters, geographic distribution, and habitat. *Anomiopsyllus hiemalis* Eads and Menzies (1948) is reduced to subspecific rank under *A. nudatus* (Baker 1898); *A. hiemalis mexicanus* (Holland 1965) is also transferred here as a subspecies of *A. nudatus*.

Phenotypic characters used to differentiate these subspecies are length and width of the movable process, distance between spiniforms of the movable process, and presence or absence of modified setae on the posterior margin of sternum IX. Measurements were made by means of a calibrated ocular grid at 430 X; the grid units were then converted to microns. Length and width measurements of the movable process were made along the longitudinal axis from the tip of the process to the "notch." The width was measured at an approximate right angle from the "notch" across the broadest part of the process. Measurements between the distal pair of spiniform setae were from center to center *at the base* of each spiniform.

Anomiopsyllus nudatus mexicanus Holland, n. comb.

Figs. 12, 35, 57, 70, 83, 94

Anomiopsyllus nudatus: Holdenreid and Morlan, 1955, J. Inf. Dis. 96: 135; Stark, 1959, Siphonaptera of Utah: 107.

Anomiopsyllus hiemalis mexicanus Holland, 1965, Canadian Ent. 97: 1056; Lewis, 1974, J. Med. Ent. 11(2): 154.

Diagnosis: Males of *A. n. mexicanus* are separable from *A. n. nudatus* and *A. n. hiemalis* by the presence of a heavy bristle at the arc of curvature of sternum IX. The movable process of the clasper is longer than in *nudatus* or *hiemalis* (M = 118 u, range 100 to 133 u) and about equal to *nudatus* in width. The distance between the distal spiniform pair is greater than in *nudatus*, but less than in *hiemalis* (M = 29 u, range 23 to 35 u).

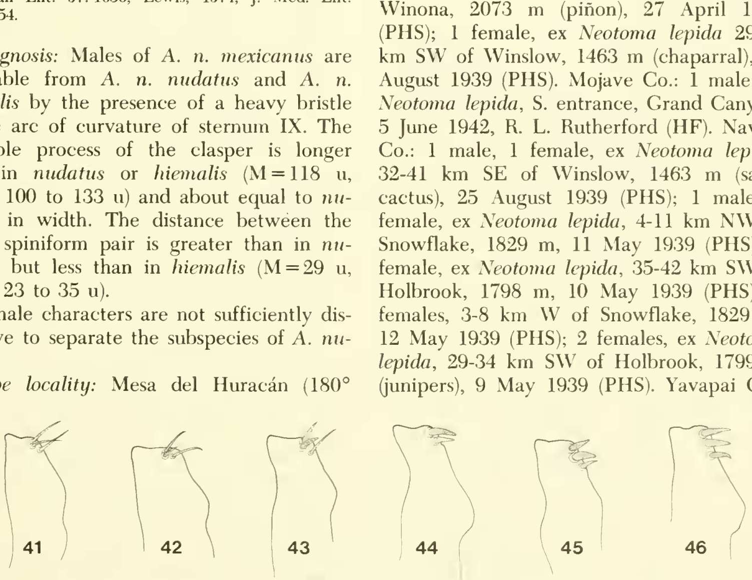
Female characters are not sufficiently distinctive to separate the subspecies of *A. nudatus*.

Type locality: Mesa del Huracán (180° 15′ W, 29° 40′ N), Chihuahua, 2256 m.

Type host: nest of *Neotoma* sp.

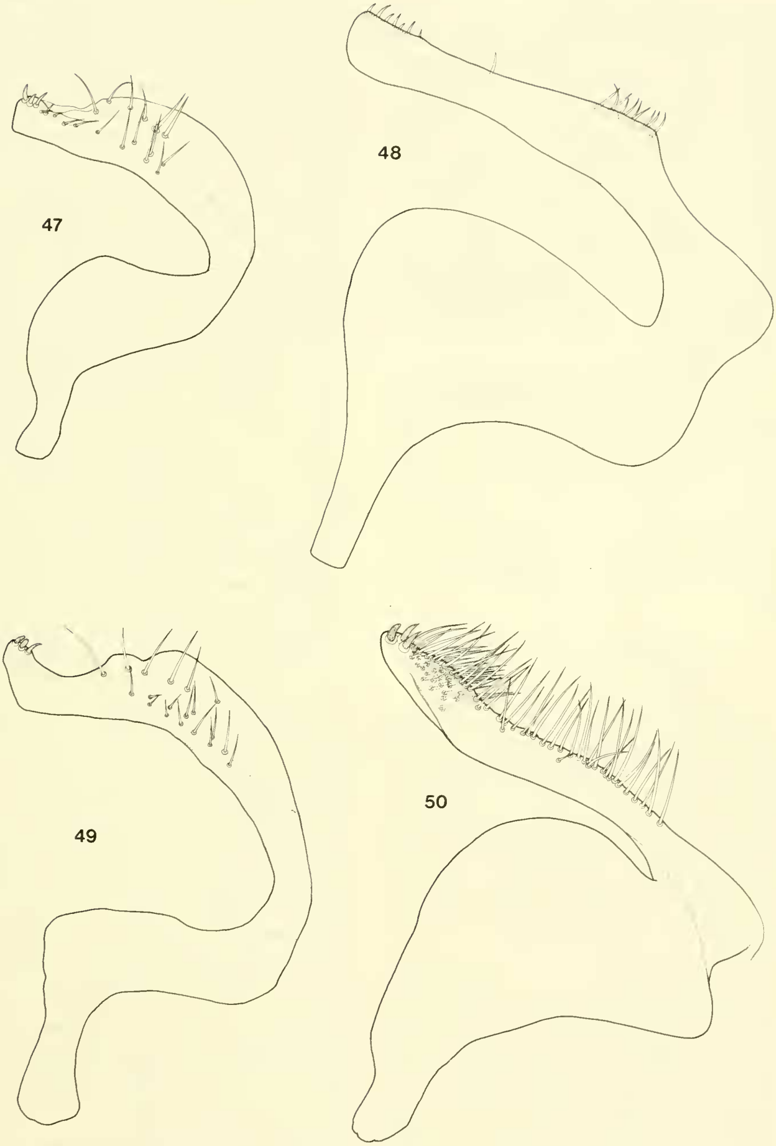
Type specimens: Male holotype and male paratype collected on 21-25 July 1964 by J. E. H. Martin, deposited in Canadian National Collection.

Material examined: Arizona: Apache Co.: 1 male, 2 females, ex *Neotoma lepida*, 44 km W of Springerville, 2302 m (cactus), 1 October 1938 (PHS); 1 male, ex *Neotoma* sp., 24 km W of Springerville, 1829 m (grass), 26 September 1938 (PHS). Coconino Co.: 1 female, ex *Neotoma albigula*, Pine Forest, 9.7 km SE of Red Lake, 2073 m (grass, cedars), 30 April 1938 (PHS); 1 male, 2 females, ex *Neotoma albigula*, 29-32 km SW of Winslow, 1463 m (chaparral), 23 August 1939 (PHS); 1 female, ex *Peromyscus maniculatus*, Pine Forest, 9.7 km SE of Red Lake, 2073 m (grass, cedars), 30 April 1938 (PHS); 1 female, ex *Peromyscus maniculatus*, 55-65 km N of Williams, 2134 m (cedar), 22 April 1938 (PHS); 1 male, ex *Neotoma lepida*, 55-60 km N of Williams, 2134 m (cedar), 22 April 1939 (PHS); 1 female, 1 male, ex *Neotoma lepida*, 3-6 km SW of Winona, 2073 m (piñon), 27 April 1939 (PHS); 1 female, ex *Neotoma lepida* 29-32 km SW of Winslow, 1463 m (chaparral), 22 August 1939 (PHS). Mojave Co.: 1 male, ex *Neotoma lepida*, S. entrance, Grand Canyon, 5 June 1942, R. L. Rutherford (HF). Navajo Co.: 1 male, 1 female, ex *Neotoma lepida*, 32-41 km SE of Winslow, 1463 m (sage, cactus), 25 August 1939 (PHS); 1 male, 1 female, ex *Neotoma lepida*, 4-11 km NW of Snowflake, 1829 m, 11 May 1939 (PHS); 1 female, ex *Neotoma lepida*, 35-42 km SW of Holbrook, 1798 m, 10 May 1939 (PHS); 3 females, 3-8 km W of Snowflake, 1829 m, 12 May 1939 (PHS); 2 females, ex *Neotoma lepida*, 29-34 km SW of Holbrook, 1799 m (junipers), 9 May 1939 (PHS). Yavapai Co.:



Figs. 41-46. Variations in apex of male ninth sternum of *A. falsicalifornicus congruens*.

4 males, 3 females, ex *Neotoma cinerea*, 22 km E of Seligman, 22 April 1938 (PHS); 1 male, ex *Neotoma cinerea*, 6 km S of Ashfork, 1585 m (rocky), 27 April 1938 (PHS); 1 male, 1 female, ex *Peromyscus* sp., 23 km E of Seligman, 1616 m, 22 April 1938 (PHS); 1 male, 1 female, ex *Peromyscus* sp., 8 km W of Seligman, 1573 m (juniper), 19 April 1938 (PHS); 3 males, ex *Peromyscus* sp., 6 km S of Ashfork 1585 m (rocky), 27 April 1938 (PHS); 2 males, 2 females, ex *Neotoma lepida*, 16 km SW of Seligman, 1585 m, 20 April 1938 (PHS); 4 males, 3 females, ex *Neotoma lepida*, 8 km NW of Clarkdale, 1067 m, 21-22 April 1938 (PHS); 3 females, ex *Neotoma lepida*, 10 km SE of Cottonwood, 23 April 1938 (PHS); 2 females, ex *Neotoma lepida*, near Wickenburg, 19 April 1938 (PHS); 2 females, ex *Neotoma albigula*, 16 km N of Paulden, W side of Verde River, 22 April 1938 (PHS), 1 male, 1 female, ex *Neotoma albigula*, 5 km NW of Dewey, 1524 m (grass, clay), 16 April 1937 (PHS) 1 male, 1 female, ex *Neotoma lepida*, 823 m, 13 April 1938 (PHS). *Colorado*: La Plata Co.: 1 female, ex *Neotoma lepida*, Hillside 10 km N of Durango, 2012 m (oaks), 13 June 1939 (PHS). Las Animas Co.: 2 males, 1 female, ex *Neotoma* sp., 5 June 1943 (PHS); 1 female, ex *Neotoma albigula*, Las Animas, 20 June 1941 (PHS). *Kansas:* Logan Co.: 1 male, 2 females, ex *Neotoma* sp., 30 May 1945 (PHS). *Nebraska:* Morrill Co.: 3 males, 2 females, ex *Neotoma albigula*, 20 May 1949 (PHS). *New Mexico:* Bernalillo Co.: 2 females, ex *Neotoma albigula*, Cedro Canyon, 3 km SE of Tijeras, 1677 m (sage, juniper), 20 May 1939 (PHS). Catron Co.: 3 males, 3 females, ex *Neotoma albigula*, 13 km N of Alma, 1524 m (juniper), 20 May 1939 (PHS); 1 male, ex *Neotoma albigula*, 3.2 km E of Alma, 1402 m (sage), 17 May 1939 (PHS); 2 males, 2 females, ex *Neotoma albigula*, 8-16 km N of Glenwood, 1402 m, 16 May 1939 (PHS); 1 male, ex *Dipodomys ordii*, 3 km E of Alma, 1402 m (sage), 17 May 1939 (PHS); 2 males, ex *Neotoma lepida*, same locality, 17 May 1939 (PHS); 1 female, ex *Spermophilus variegatus*, between Pleasanton and Mogollon, 1829-2134 m (grass), 25 April 1939 (PHS); 1 female, ex *Peromyscus truei*, 1.6-4.8 km S of Pleasanton, 1402 m (juniper), 19 May 1939 (PHS); 1 male, 2 females, ex *Neotoma mexicana*, 10 km NE of Adams Diggings, 2287 m (prairie, junipers) 16 August 1938 (PHS); 1 female, ex *Neotoma mexicana*, Cibola Forest, 10 km W of Datil, 2439 m (juniper), 20 August 1938 (PHS); 1 female, ex *Neotoma mexicana*, 1.6 km SW of Datil, 2378 m (range, juniper), 24 August 1938 (PHS). Colfax Co.: 1 female, ex *Neotoma* sp., 4 June 1943 (PHS). Grant Co.: 2 males, ex *Peromyscus eremicus*, 3-11 km NW of Silver City, 1829 m (grass), 25 April 1939 (PHS); 1 male, 9 females, ex *Neotoma albigula*, Fort Bayard Reservation, 1829 m (grass), 28 April 1939 (PHS); 1 male, 7 females, ex *Neotoma albigula*, 3-11 km NW of Silver City, 1829 m (brush), 29 April 1939 (PHS); 6 males, ex *Neotoma albigula*, 19-22 km SE of Silver City, 1768 m (juniper), 27 April 1939 (PHS), 1 male, 1 female, ex *Neotoma albigula*, 6-8 km NW of Silver City, 1829 m (cactus), 22 April 1939 (PHS); 1 female, ex *Dipodomys merriami*, 19-22 km SE of Silver City, 1768 m (juniper), 27 April 1939 (PHS). Lincoln Co.: 2 males, 2 females, ex *Neotoma albigula*, 43 km E of Capitan, 1936 m (rocky timber), 18 April 1949 (PHS). Rio Arriba Co.: 1 male, ex *Peromyscus* sp., 5 km W of Coyote, 2591 m (timber), 10 June 1949 (PHS). San Miguel Co.: 1 male, 1 female, ex *Peromyscus* sp., Pecos, 22 February 1941, McMurray (RM). Sante Fe Co.: 14 males, 6 females, ex *Neotoma albigula* nests, Steel Ranch, November and December 1951, H. B. Morlan, 5 males, 10 females, ex *Neotoma albigula*, 23-25 May 1939 (PHS); 1 male, ex *Peromyscus maniculatus*, same locality, 23 May 1939 (PHS). Sierra Co.: 1 male, ex *Neotoma albigula*, 8-9.6 km S of Hillsboro, 1555 m (sandy), 28 June 1939 (PHS); 1 female, ex *Neotoma albigula*, Canyon, 6 km W of Hillsboro, 1677 m (cactus), 18 April 1939 (PHS); 2 males, 6 females, ex *Neotoma albigula*, Range, 3 km E of Winston, 1677 m (juniper), 21 April 1939 (PHS). Socorro Co.: 1 male, 2 females, ex *Neotoma albigula*, 4.8-8 km NW of Magdalena, 2403 m (juniper), 23 June 1939 (PHS) (type series); 1 male, ex *Neotoma albigula*, 3-6 km NW of Magdalena, 2403 m (juniper), 22 June 1939 (PHS); 1 male, 1 fe-



Figs. 47-50. Male ninth sternum: 47, *A. durangoensis*; 48, *A. traubi* (redrawn from Barrera 1951 and Barnes 1963); 49, *A. novomexicanensis*; 50, *A. oaxacae*.

male, ex *Neotoma albigula*, 16 km W, 9.6 km N of Magdalena, 2348 m, 6 May 1948 (PHS). Taos Co.: 1 female, ex *Neotoma mexicana*, 27 km S of Taos, 1829 m (sage, juniper), 17 August 1948 (PHS). Valencia Co.: 1 male, 1 female, ex *Neotoma* nest, 11 km SE of El Morro (lava outcrop), 14 June 1950 (PHS). *Utah:* Beaver Co.: 2 males, ex *Neotoma* sp., 8 May 1945 (PHS); 1 female, ex rodent nest, 16 km W of Beaver, 2134 m, 7 May 1949 (PHS). Garfield Co.: 1 male, 1 female, 6 km S of Panguitch, 2043 m (juniper), 29 April 1949. *Wyoming:* Albany Co.: 1 male, 1 female, ex *Neotoma cinerea*, 10 July 1944 (PHS); 3 females, ex *Neotoma* sp., 8 July 1943 (PHS).

Discussion: Anomiopsyllus n. starki, a nomen nudum described by Barnes in his doctoral dissertation in 1963, is the same in all morphological characters and measurements as *A. n. mexicanus. Anomiopsyllus n. mexicanus* represents a form intermediate between *A. n. nudatus* and *A. n. hiemalis*, as indicated by Barnes in his description of *A. n. starki.* Measurements (males) given by Barnes were based on specimens of *A. n. starki.*

Anomiopsyllus nudatus hiemalis Eads and Menzies n. comb.

Figs. 10, 34, 56, 69, 82, 94

Anomiopsyllus hiemalis Eads and Menzies, 1948, J. Kans. Ent. Soc. 21(4): 133-136; Eads and Menzies, 1950, Texas State Hlth. Dept. 53; Jellison, Locker, and Bacon, 1953, Index to the literature of Siphonaptera of North America, Suppl. 1: 11; Vargas, 1960, Med. Rev. Mexicana 40 (849) 1-4; Poorbaugh and Gier, 1961, J. Kans. Ent. Soc. 34(4): 200; Jellison and Glesne, 1967, Index to the literature of Siphonaptera of North America, Suppl. 2: 13-19; Pratt and Stark, 1973, DHEW Publ. 74-8267: 11.

Anomiopsyllus hiemalis hiemalis: Holland, 1965, Canadian Ent. 97: 1055-1056; Lewis, 1974, J. Med. Ent. 11(2): 154.

Diagnosis: Males of *A. n. hiemalis* are distinguished from *A. n. nudatus* by the wide space between the distal pair of spiniforms on the movable process (greater than 20 u), and from *A. n. mexicanus* by the presence of a slender bristle at the arc of curvature of sternum IX. The movable process in *hiemalis* is shorter than in *nudatus* or *mexicanus* (M = 107 u, range 97 to 112 u), but broader than both (M = 81 u, range 73 to 94 u). The distance between the distal pair of spiniforms closely overlaps that of *mexicanus* (M = 35 u, range 16 to 42 u), but the two species may be distinguished by the thin bristle on sternum IX.

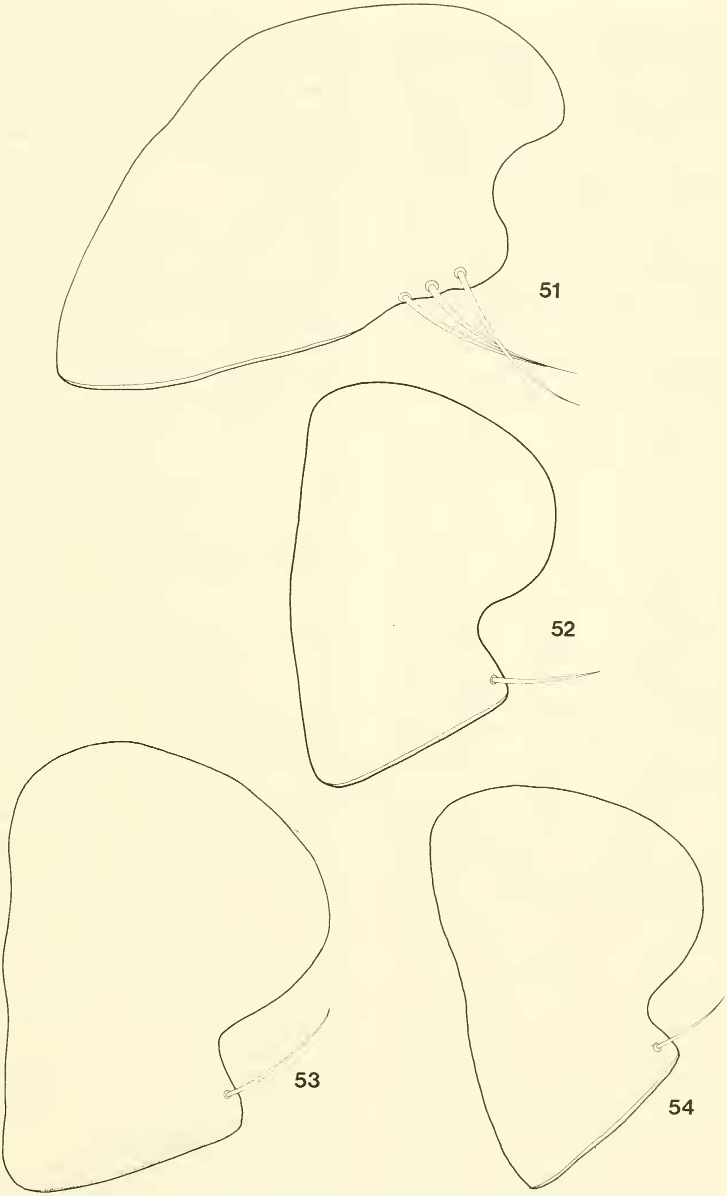
Female characters are not sufficiently distinctive to separate the subspecies of *A. nudatus.*

Type locality: Gaines County, Texas.

Type host: Neotoma micropus Baird

Type specimens: Male holotype and female allotype collected on 23 and 9 (respectively) April 1948 by V. I. Miles, deposited in U.S. National Museum.

Material examined: Colorado: Baca Co.: 1 male, 1 female, ex *Neotoma albigula*, 6 km N of Pritchett, 1341 m, 11 May 1948 (PHS). Pueblo Co.: 1 male, ex *Neotoma* sp., 6 August 1948 (PHS). Yuma Co.: 1 male, 1 female, ex *Neotoma albigula*, 1.6 km S, 6 km W of Wray, 1068 m, 10 July 1948 (PHS). *Kansas:* Barber Co.: 1 male, 1 female, ex *Neotoma micropus*, 5.6 km S, 1.6 km W of Aetna, 13 April 1949, Loomis and Lipovsky (RM); 18 males, 23 females, ex *Neotoma micropus*, 8 km S of Aetna, no date, Hopla and Loomis (U.O.); 41 males, 89 females, ex *Neotoma micropus*, Hopla (U.O.). Clark Co.: 1 male, 1 female, ex *Neotoma micropus*, 15 May 1942 (PHS). Gove Co.: 3 females, ex *Neotoma* sp., 7 September 1946 (PHS). Meade Co.: 1 female, ex *Neotoma micropus*, 12 May 1942 (PHS); 1 female, ex *Sigmodon hispidus*, 19 km S of Meade, 10 May 1950 (PHS). Seward Co.: 1 male, 1 female, ex *Neotoma micropus*, 15 May 1942 (PHS). *New Mexico:* Chavez Co.: 2 males, 2 females, ex *Neotoma albigula*, 8 km E of Haggerman, 1037 m (mesquite), 13 April 1948 (PHS); 1 male, 1 female, ex *Neotoma albigula*, 11 km E of Haggerman, 1158 m, 8 April 1948 (PHS). Eddy Co.: 2 males, 2 females, ex *Neotoma albigula*, 8 km E of Artesia, 1158 m (mesquite), 24 March 1949 (PHS); 1 female, ex *Neotoma albigula*, 3 km W of Loco Hills, 1006 m (yucca, mesquite), 16 February 1950 (PHS). Lea Co.: 1 male, ex *Neotoma albigula*, 6 km N, 31 km E of Lovington, 1220 m, 25 March 1949 (PHS); 4 males, 4 females, ex *Neotoma* nest,.8 km N of Hobbs, 1006 m (mesquite), 22 February 1950 (PHS). *Oklahoma:* Caddo



Figs. 51-54. Male eight sternum: 51, *A. nidiophilus*; 52, *A. amphibolus*; 53, *A. montanus*; 54, *A. sinuatus*.

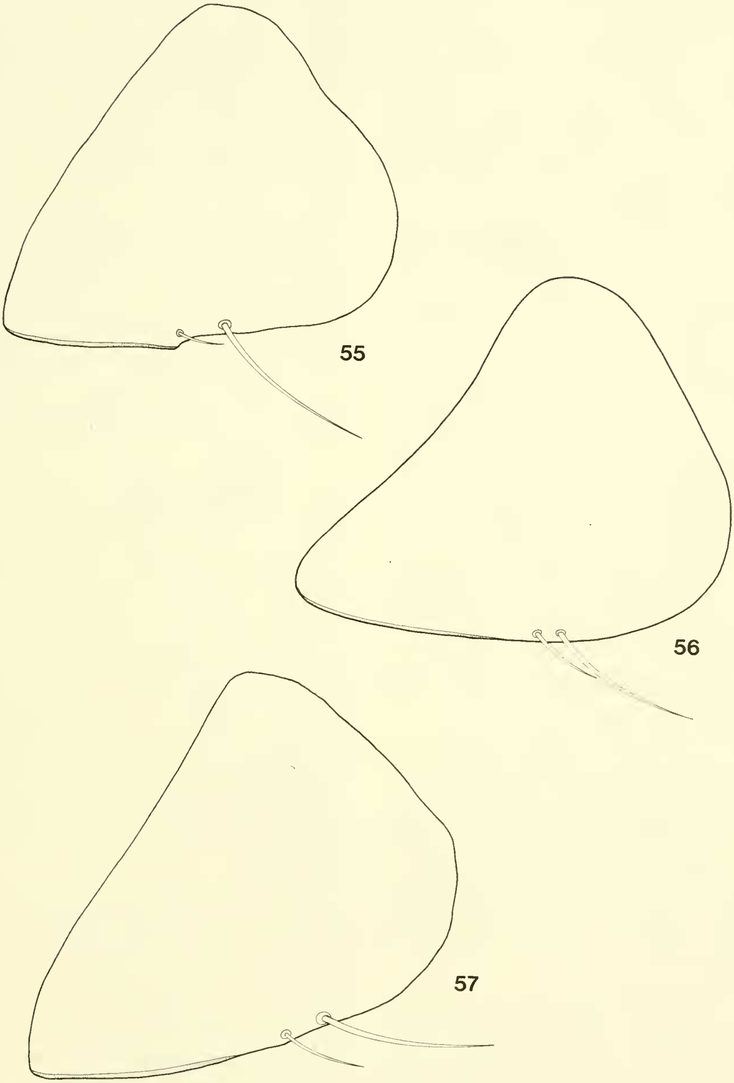
Co.: 2 males, 2 females, ex *Neotoma micropus* nest, April 1958, T. Emerson (U.O.). Herman Co.: 5 males, 16 females, ex *Neotoma micropus* nests, April 1960, C. J. Mitchell (U.O.). Texas Co.: 1 male, ex *Neotoma albigula*, 9.7 km E of Hardesty, 945 m (yucca, sagebrush), 9 May 1950 (PHS). *Texas:* Bailey Co.: 1 female, ex *Neotoma* sp., Muleshoe, 3 March 1957, Simmons. Brewster Co.: 1 male, ex *Neotoma mexicana*, 20 April 1942 (PHS); 2 females, ex rodent nest, Big Bend National Park, 31 October 1963, V. J. Tipton; 1 male, ex *Neotoma micropus* nest, Big Bend National Park, 2 November 1948, V. J. Tipton; 1 male, 1 female, ex *Peromyscus pectoralis*, Big Bend National Park, 10 April 1963, V. J. Tipton. Coke Co.: 3 females, 1 male, ex *Neotoma albigula*, 29 April 1942 (PHS). Crane Co.: 1 male, ex *Neotoma albigula*, 29 April 1942 (PHS). Dawson Co.: 1 male, 1 female, ex *Neotoma micropus*, 11 February 1948 (PHS); 1 female, ex *Neotoma micropus*, 2 November 1948, Miles. Ector Co.: 2 males, 1 female, ex *Neotoma floridana*, 26 km W of Odessa, 884 m (mesquite, yucca), 15 April 1960 (PHS). Hartley Co.: 4 males, 3 females, ex *Neotoma micropus*, October 1944 (PHS). Hutchinson Co.: 3 males, 1 female, ex *Neotoma micropus*, 31 May 1944 (PHS); 1 male, 1 female, ex *Neotoma micropus*, 9.7 km W of Electric City (mesquite), 2 May 1950 (PHS). Jeff Davis Co.: 1 male, 1 female, ex *Neotoma mexicana*, 2 May 1942 (PHS). Knox Co.: 1 male, 1 female, ex *Neotoma mexicana*, 16 October 1946 (PHS). Motley Co.: 1 male, 1 female, ex *Neotoma albigula*, 3 October 1946 (PHS). Pecos Co.: 1 male, ex *Dipodomys spectabilis*, 21 April 1942 (PHS). Terrell Co.: 1 male, ex *Neotoma albigula*, 1 April 1942 (PHS). Tom Green Co.: 3 males, 1 female, ex *Neotoma* sp., 11 April 1947 (PHS). Ward Co.: 2 males, 2 females, ex *Neotoma albigula*, 5 April 1948 (PHS). *Mexico:* Coahuila D. F.: 2 males, 2 females, ex *Neotoma micropus*, Sabinas, 20 September 1944, A. Dampf (RM); 1 male, 1 female, same locality, no date, T. Mazzotti (RM); 2 males, 2 females, same locality, 30 August 1944 (PHS); 1 male, 1 female, ex *Neotoma* nest, same locality, 1 October 1944 (RT).

Discussion: Eads and Menzies (1948) in describing *A. hiemalis* noted the close relationship to *nudatus*, and differentiated their species primarily by the greater distance between the distal spiniforms of the movable process in *hiemalis*. They stated that the movable process is "... broad and conical." The breadth of the process was considered diagnostic.

Stark (1959) reported the existence of atypical *nudatus* in western Utah, noting the greater distance between spiniforms in his atypical specimens as compared to the typical *nudatus*. Stark also noted that sternum IX of males in his atypical specimens varied from typical *nudatus*, but did not give any details. *Anomiopsyllus nudatus mexicanus* is intermediate between *A. nudatus nudatus* and *A. nudatus hiemalis* with respect to distance between spiniforms, but distinct from either by virtue of several modified setae dorsomedially on the posterior margin of male sternum IX. It is also intermediate geographically, its range falling between the eastern *hiemalis* and the western *nudatus*. In regard to length and breadth of the movable process, *A. n. mexicanus* is more like *nudatus* than like *hiemalis*. The process of *mexicanus* is apparently longer in relation to width than that of *hiemalis*, thus less "conical."

Exhaustive examination of specimens available for study has not resulted in finding characters other than those mentioned. The morphology of the populations is subject to remarkably little variation except in the male external genitalia. Other possible characters thoroughly investigated were: setation of head, thorax, and abdomen; shape of thoracic segments and setation of legs; potential difference in proportion of tarsal segments; and both male and female genitalia. No other consistent variations were found. The females are apparently not separable, although a trend exists toward a deeper sinus in the posterior margin of tergum VIII of *A. n. hiemalis*. The sinus is used as a key character for *hiemalis* by Hopkins and Rothschild (1962).

To examine the relationships of the three groups, a series of measurements was taken as follows: (1) width of the movable process



Figs. 55-57. Male eight sternum: 55, *A. nudatus nudatus*; 56, *A. nudatus hiemalis*; 57, *A. nudatus mexicanus*.

from the "notch" above the point of articulation across the broadest portion of the lower lobe; (2) length of the process from its tip to the "notch"; (3) distance from center to center between the spiniforms. The manner in which measurements were made is illustrated in Figure 93. The measurements were taken with a calibrated ocular grid, using 10X eyepiece and 43X objective with grid units converted to microns (0.1 grid units = 1.624 u).

Due to the allopatric nature of the populations, *mexicanus*, the geographically central population, was compared first to *hiemalis* and then to *nudatus*. If each of the two populations is related to *mexicanus*, then they are related to one another. *Anomiopsyllus n. mexicanus* and *hiemalis* are closely linked by the overlap of distances between spiniforms, yet separated by length and width of the movable process. *Anomiopsyllus n. mexicanus* and *nudatus* are sharply distinguished by distance between spiniforms, but with significant overlap in length of process, and they almost completely overlap in width of process. *Anomiopsyllus n. mexicanus* is further distinguished from both *hiemalis* and *nudatus* by presence of modified setae (Figs. 24, 25) of sternum IX in males.

The *A. nudatus* complex ranges from western Kansas, Oklahoma, and Texas south to Sabinas, Coahuila, Mexico, and west to the Pacific Coast of southern California.

The subspecies *A. nudatus nudatus*, the westernmost representative of the three subspecific populations, has a primarily Sonoran Desert distribution (Shreve and Wiggins 1951; Map 2). Its range is not limited to the Sonoran Desert, but occurs in a variety of habitats occupied by its wood rat hosts; e.g., in pine-fir forest at 2134 m elevation in the San Bernardino Mountains of southern California.

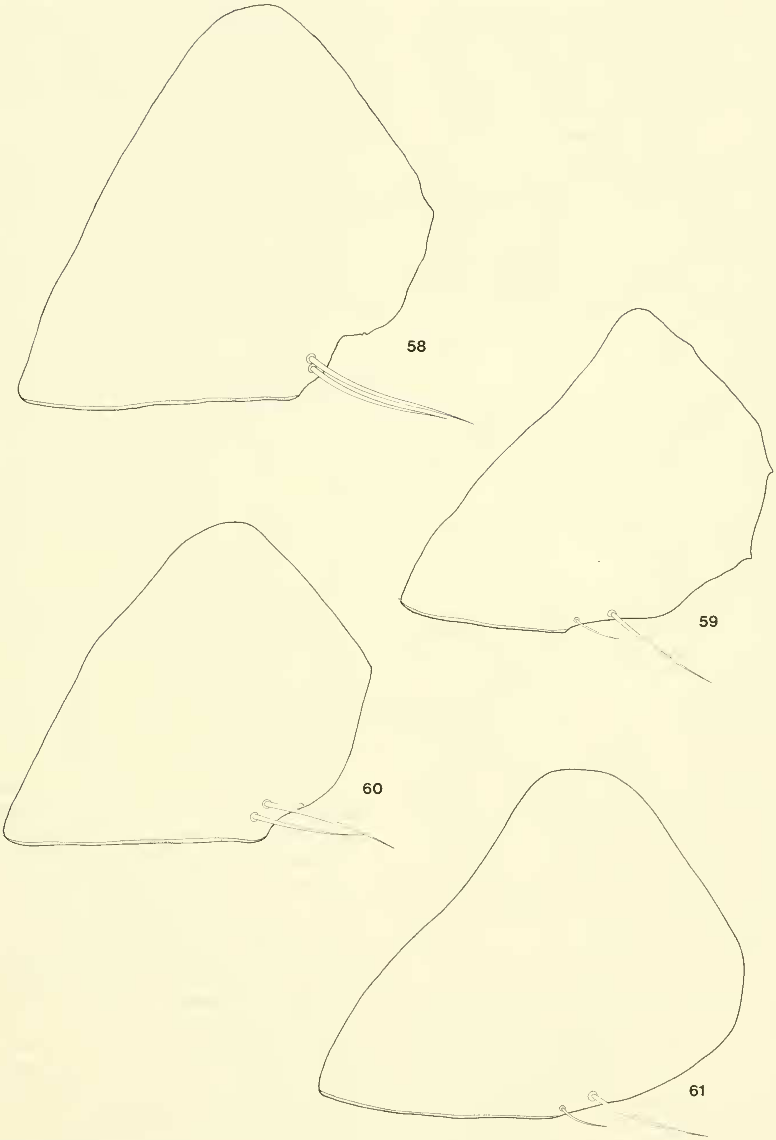
In southern California, *A. n. nudatus* is found in coastal chaparral and oak woodland bordering the sea as well as in its typical desert habitat. In the Santa Monica Mountains and parts of the San Gabriel Mountains of Los Angeles County, it is replaced by *A. falsicalifornicus* in moister oak woodland and chaparral situations. In the Los Angeles area, the distributions of *A. n. nudatus* and *A. falsicalifornicus* interdigitate: *nudatus* occurs in drier areas where yucca and cactus grow, and *falsicalifornicus* occurs in moister areas characterized by *Rhus diversiloba* and *Photinia*. This situation continues northward to Ventura County, California, where *nudatus* occupies the arid habitat in the rain shadow south and east of the southern Santa Ynez Mountains.

From Ventura County eastward, *nudatus* is recorded from the area of Frazier Park, Kern County, and the Antelope Valley of northern Los Angeles County. It is replaced above the lower, winter snow line by *A. walkeri* in the Tehachapi and southern Sierra Nevada Mountains. From this point it occurs across the Mojave and Sonoran deserts, its distribution including the southwest corner of Nevada and Sonoran Desert areas of Arizona.

Areas where the distribution of *n. nudatus* is doubtful include the northern portions of the Mojave Desert and arid areas on the west side of the southern San Joaquin Valley in California where collections of wood rat nests made by the senior author have been negative for *Anomiopsyllus*. Several females, collected by R. Ryckman from the San Pedro Martir Mountains of Baja California, are probably *A. n. nudatus*. A collection of 20 wood rats (*Neotoma albigula*) near Hermosillo, Sonora, Mexico, by K. Murray and H. Johnson during March and April, 1960, failed to produce *Anomiopsyllus*. *Anomiopsyllus n. mexicanus* was collected in central Mexico by J. E. H. Martin during July 1964 from a nest of *Neotoma* sp.

In Arizona, the distribution of *A. n. nudatus* is sharply interrupted along the escarpment of the Colorado Plateau by the presence of a central subspecies, *A. n. mexicanus*. In San Juan County, southeastern Utah, *A. n. nudatus* makes a deep incursion into the area occupied by *A. n. mexicanus* (Map 2), a situation further discussed under that subspecies.

The distribution of *A. nudatus mexicanus* lies within the Basin and Range Province as defined by Shreve and Wiggins (1951). In



Figs. 58-61. Male eight sternum: 58, *A. falsicalifornicus congruens*; 59, *A. walkeri*; 60, *A. falsicalifornicus falsicalifornicus*; 61, *A. martini*.

Arizona, its boundaries coincide with the edge of the Sonoran Desert and the occurrence of *A. nudatus nudatus*. In the east, its range is interrupted by the western edge of the Great Plains (High Plains, according to Webb 1951) and the presence of *A. n. hiemalis*. Its northern range is indented by the central Rocky Mountain mass. A narrow band just east of the Rockies carries the subspecies through far eastern Colorado and western Kansas to Morrill County, Nebraska, and Albany County, Wyoming. In southcentral New Mexico, it is absent from the lower Chihuahuan Desert habitat, where it is replaced by *A. novomexicanensis*, as *A. n. mexicanus* appears to occupy the higher elevations.

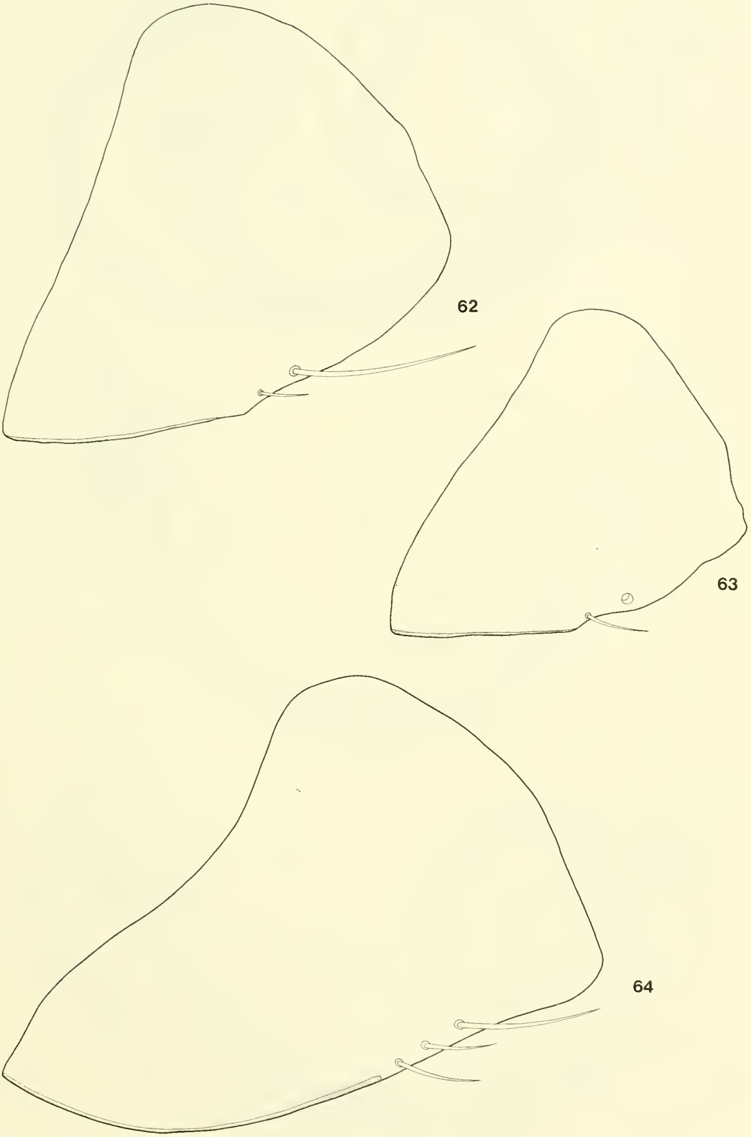
In Utah, a confusing picture is presented by the occurrence of *nudatus nudatus* in San Juan County in the southeastern corner of the state. Stark (1959) reported atypical *nudatus* from Millard, Beaver, and Garfield counties in Utah and typical *nudatus* in San Juan County. Examination of his specimens shows the former to be *n. mexicanus* and the latter *n. nudatus*. It is suspected that barriers such as the Colorado River in the west and discontinuous wood rat distribution to the east may explain the disjunct distribution observed in *n. nudatus*. In San Juan County, only *n. nudatus* has been collected; however, west of the Colorado River in Utah, only *n. mexicanus* has been collected. Two of the San Juan *n. nudatus* collections are from high elevations in habitats similar to those preempted by *n. mexicanus* along the Colorado Plateau escarpment where the two subspecies are known to meet. Collections in the rugged area of southcentral Utah and northcentral Arizona are needed to clarify the *n. mexicanus* distribution.

Anomiopsyllus n. hiemalis replaces *A. n. mexicanus* at lower elevations at the eastern and southwestern edge of the *n. mexicanus* distribution. The distributions of the two subspecies interdigitate where plains are intersected by spurs of the Rockies (see *novomexicanensis* for further discussion). Intergrades between *n. mexicanus* and *n. hiemalis* occur in Santa Fe and San Miguel counties, New Mexico, and specimens assignable to each subspecies have been taken in the same area in Santa Fe County by U.S.P.H.S. field workers. In eastern New Mexico and Colorado where apparent overlap occurs, *n. hiemalis* occupies the habitat below 1341 m elevation and *n. mexicanus* occupies the higher elevations.

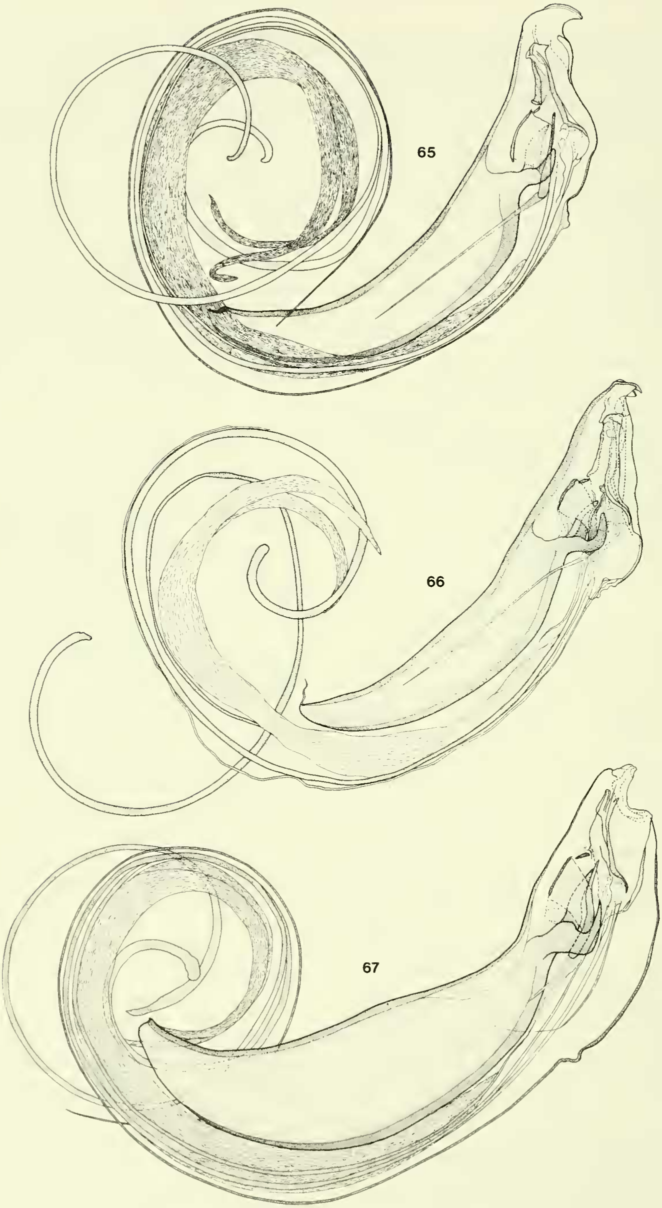
The range of *A. n. hiemalis* falls primarily into two biotic areas defined by Webb (1951) as the High Plains and Trans-Pecos areas and by Dice (1943) as the Kansan and Tamaulipan. These areas are characterized by moderate elevation (generally below 1220 m) and low annual rainfall (50 cm or less). Where vegetation type has been noted on *n. hiemalis* slides examined, mesquite (*Prosopis* sp.) predominates. Geographically, the area occupied by *n. hiemalis* includes southwestern Kansas, western Oklahoma and Texas, extreme eastern Colorado, and New Mexico south to Sabinas, Coahuila D. F., Mexico. The northernmost record noted is Yuma County, Colorado, and the easternmost are Barber County, Kansas, and Caddo County, Oklahoma.

As was speculated earlier for *n. nudatus*, the ranges of all three subspecies probably extend south into Mexico. The lack of specimens from Mexico precludes an accurate estimate, but the habitats occupied in the United States also occur in Mexico. Shreve and Wiggins (1951) shows Sonoran Desert, the habitat occupied by *n. nudatus*, as occurring west of the Sierra Madre Occidental as far south as the Río Yaqui. The upland habitat preferred by *n. mexicanus* extends south along the continental divide (Brand 1936, Leopold 1950). The mesquite scrub, characteristic of *n. hiemalis* habitat in Texas, extends south into eastern Mexico.

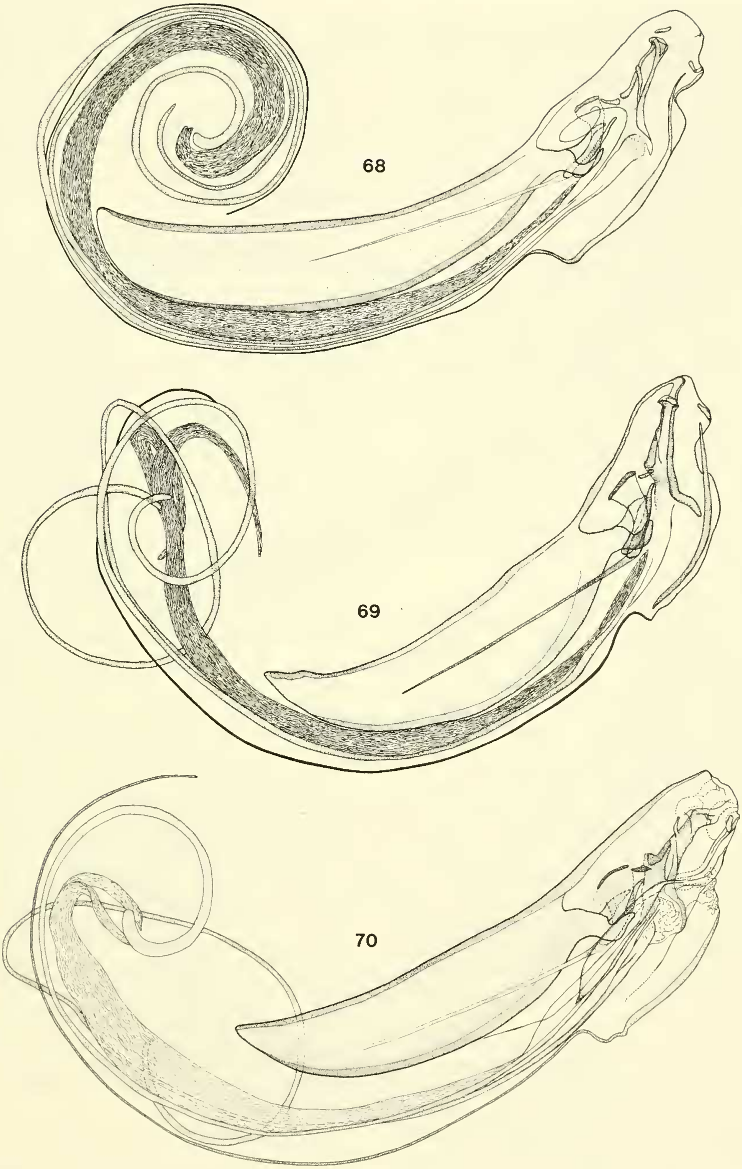
The apparent replacement of one subspecies by another with great changes in topography and habitat is strongly suggestive of similar phenomena noted with other *Anomiopsyllus* species. In California, where extensive field collecting was done in this study, *A. nudatus* was found to be replaced by *A. walkeri* at higher elevations in the Tehachapi Mountains and by *A. falsicalifornicus* in more mesic environments (i.e., rainfall over 50 cm/year). The phenomenon of displacement may be understood ultimately



Figs. 62-64. Male eight sternum: 62, *A. novomexicanensis*; 63, *A. durangoensis*; 64, *A. oaxacae*.



Figs. 65-67. Aedeagus: 65, *A. sinuatus*; 66, *A. montanus*; 67, *A. nidiophilus*.



Figs. 68-70. Aedeagus: 68, *A. nudatus nudatus*; 69, *A. nudatus hiemalis*; 70, *A. nudatus mexicanus*.

through laboratory studies or the range of tolerance for physical climate factors or by further field studies involving several of the species. The response to climate is not the only limiting factor involved in distribution of *Anomiopsyllus* species. This is illustrated by those species or subspecies that are capable of occupying a broad spectrum of climatic conditions in the absence of related species or subspecies. *Anomiopsyllus n. nudatus* occurs at elevations up to 2195 m in California and is displaced by *A. n. mexicanus* at higher elevations in Arizona and *A. walkeri* in California as noted above.

Hosts: Anomiopsyllus nudatus subspecies are restricted to wood rats (*Neotoma* spp.) as major hosts and seldom occur on other rodents. In the material examined, fortuitous hosts are probably more numerous than normally occur in nature. Many of these records result from plague surveys in which most of the specimens were ground and inoculated into test animals, and collectors often tended to retain specimens from odd hosts for the record.

Within the habitats occupied by *A. nudatus*, its subspecies occur indiscriminately on available wood rat species, with the exception of *Neotoma cinerea* which Goldman (1910) and Hall and Kelson (1959) place in a separate subgenus, *Teonoma*. *Neotoma floridana* is primarily a resident of moist eastern deciduous forest communities. Its distribution extends through western Kansas and northeastern Colorado where it occupies situations characteristic of *N. albigula* such as cactus huts (Warren 1942). In Colorado, Finley (1958) has recorded *Anomiopsyllus* sp. from *N. floridana*, but his specimens have not been available for study. On the other hand, Rainey (1956), and Ellis (1955) did not record *Anomiopsyllus* from *N. floridana* in eastern Oklahoma.

The range of *A. nudatus* or any of its subspecies never coincides with the range of any one wood rat species. Thus, in southern California, *nudatus nudatus* occurs on both *N. lepida* and *N. fuscipes* in arid situations, while in less arid areas the same two hosts are parasitized by different *Anomiopsyllus* species. In Arizona and New Mexico the range of *N. mexicana* appears to limit the range of *A. n. mexicanus*, but the *N. mexicana* range is exceeded by the range of *A. n. mexicanus* in western Utah where the flea occurs on *N. lepida*. Within the range of the host genus *Neotoma*, *A. nudatus* subspecies are apparently limited by factors other than host occurrence as are other *Anomiopsyllus* spp.

Anomiopsyllus falsicalifornicus Fox

Figs. 14, 15, 37, 40, 58, 60, 71, 72, 85, 86, 95

Anomiopsyllus californicus: Fox, 1926 (*nec* Baker, 1904), Pan-Pacific Ent. 2: 183; Wagner, 1930, Mag. Parasitol. Moscow 1: 135.

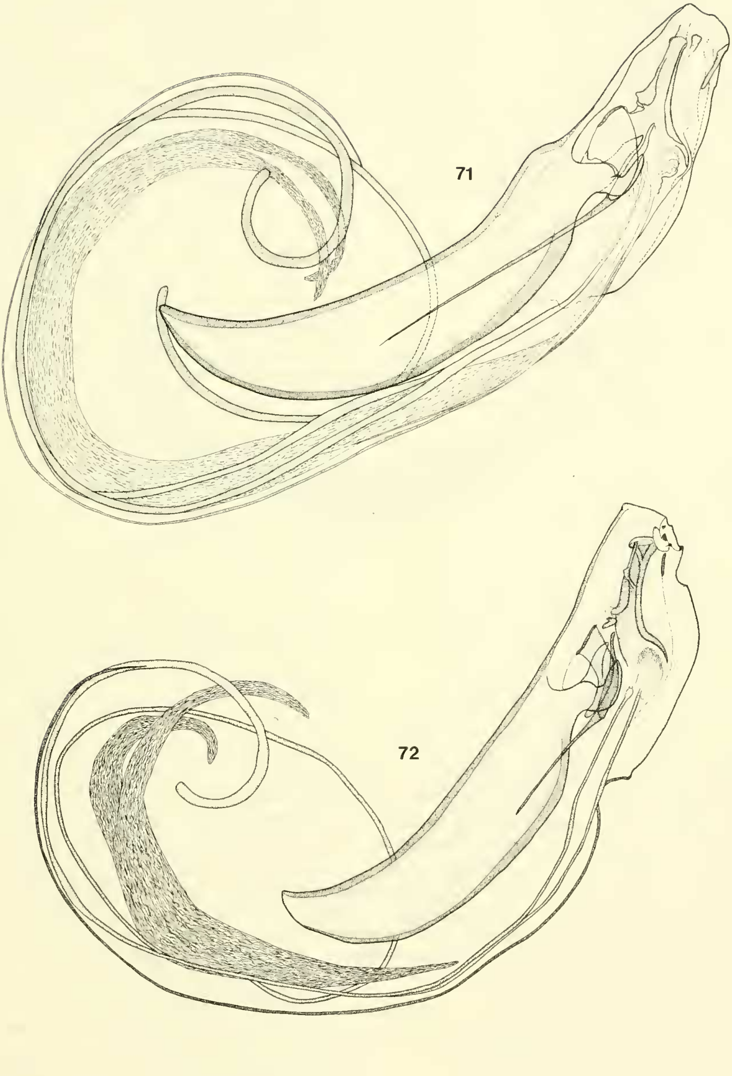
Anomiopsyllus falsicalifornicus Fox, 1929, Ent. News 40: 218; Collins, 1936, Ent. News 47: 130; Hubbard, 1947, Fleas of western North America: 78-80; Linsdale and Davis, 1956, Univ. Calif. Publ. Zool. 54: 306-308; Holland, 1965, Canadian Ent. 97: 1052; Barnes, 1965, Pan-Pacific Ent. 41(4): 278; Coultrip et al., 1973, J. Med. Ent. 10(3): 306.

Diagnosis: Anomiopsyllus falsicalifornicus is separable from other species (males) by the suboblique row of three spiniform setae near the apex of the movable process coupled with the presence of only 0-3 spiniforms at the apex of the distal arm of sternum IX. The movable process is roughly triangular with always some degree of concavity (shallow to extreme) on the posterior margin below the distal spiniform row. The anterior margin is linear, tipped slightly anterad at the subacute apex with three heavy spiniforms near the apex with or without a small spiniform near the posterior margin of the basal lobe. The proximal arm of sternum IX is similar to *nudatus*. The distal arm is variable in shape and the apex rounded or flattened with 0-3 heavy setae at the apex and a row of 4-6 moderately heavy setae mesad on the posterior margin.

Females are similar to *nudatus* but can be separated by the presence of the sclerotized portion of the blind ductus seminalis (Fig. 72, 76). Female characters are not sufficiently distinctive to separate subspecies of *falsicalifornicus*.

Average Length: Male 1.6 mm; female 1.9 mm.

Type locality: Claremont, Los Angeles County, California



Figs. 71-72. Aedeagus: 71, *A. walkeri*; 72, *A. martini*.

Type host: Neotoma fuscipes and *Spilogale phenax*

Type specimens: Male holotype deposited in the U.S. National Museum.

Fox (1926) first described the male of this species, believing it to be *A. californicus* Baker, a species that had been described from near Claremont, California. Jordan and Rothschild (1915) examined Baker's syntypic series of females and entered *californicus* into synonomy with *nudatus*. Fox (1929), acting on information from Jordan, then gave his male specimen the name *falsicalifornicus*.

Anomiopsyllus falsicalifornicus is treated here as two subspecies: *A. f. falsicalifornicus, A. f. congruens*.

Anomiopsyllus falsicalifornicus congruens Stewart

Figs. 15, 40, 58, 71, 85, 95

Anomiopsyllus congruens Stewart, 1940, Pan-Pacific Ent. 16: 17-18; Hubbard, 1940, Pac. Univ. Bull. 37(4); Hubbard, 1943, Pac. Univ. Bull. 39(8): 1-12; Augustson, 1943, Bull. South. Calif. Acad. Sci. 42: 69; Hubbard, 1947, Fleas of western North America: 81–82; Jellison, Locker, and Bacon, 1953, Index to the literature of Siphonaptera of North America, Suppl. 1: 10; Linsdale and Davis, Univ. Calif. Publ., Zool. 54(5): 306-308; Holland, 1965, Canadian Ent. 97: 1052, Barnes, 1965, Pan-Pacific Ent. 41(4): 278.

Anomiopsyllus falsicalifornicus congruens Hopkins, 1952, J. Wash. Acad. Sci. 42(11): 365; Holland 1965, Can. Ent. 97: 1053; Jellison and Glesne, 1967, Index to the literature of Siphonaptera of North America, Suppl. 2-13: 19; Lewis 1974, J. Med. Ent. 11(2): 154.

Diagnosis: The males of *A. f. congruens* are distinguished from *A. f. falsicalifornicus* by the narrow sternum IX with an angulate, truncate apex. The fixed process of the clasper is broader than long. Sternum IX is only one-third to one-half as broad mesally as in *f. falsicalifornicus* and is equipped apically with 1, 2, or 3 heavy setae. The movable process is similar to *f. falsicalifornicus* but possesses a proximal spiniform.

Female characters are not sufficiently distinctive to separate subspecies of *falsicalifornicus*.

Type locality: Frances Simes Hastings Natural History Reservation near Jamesburg, Monterey County, California.

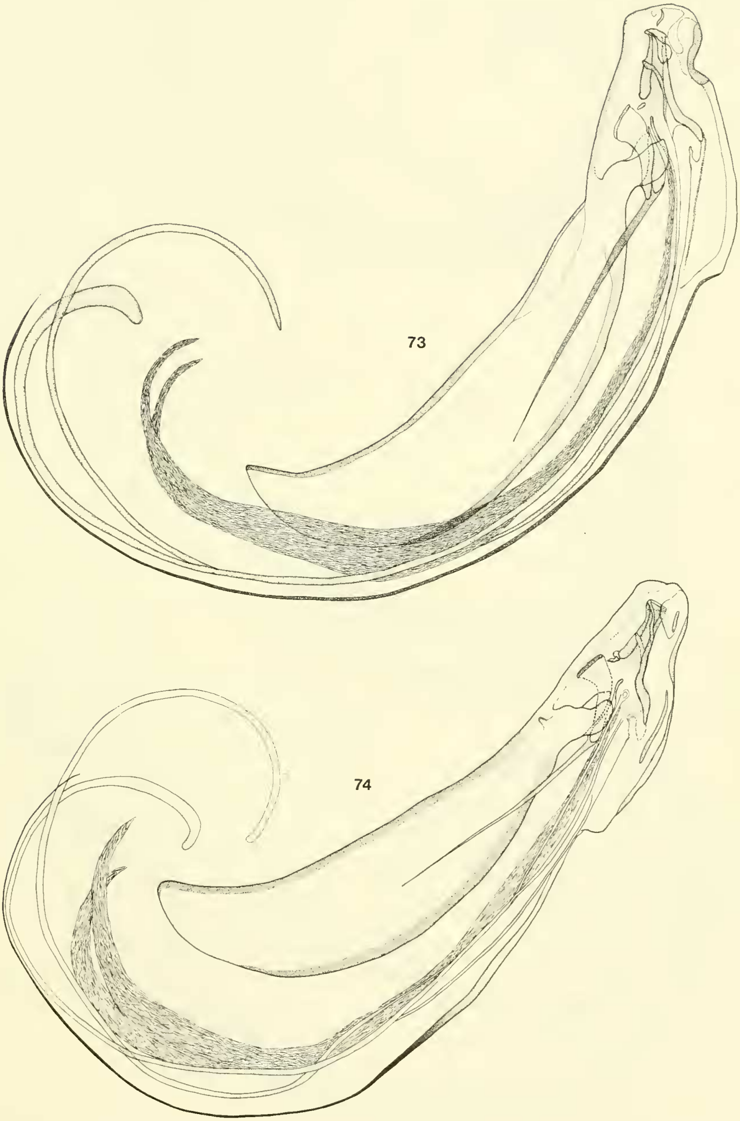
Type host: Spilogale gracilis ssp.

Type specimens: Holotype male and allotype female collected on 19 November 1938 by R. Holdenried, deposited in Museum of the California Insect Survey, Univ. of California, Berkeley, California.

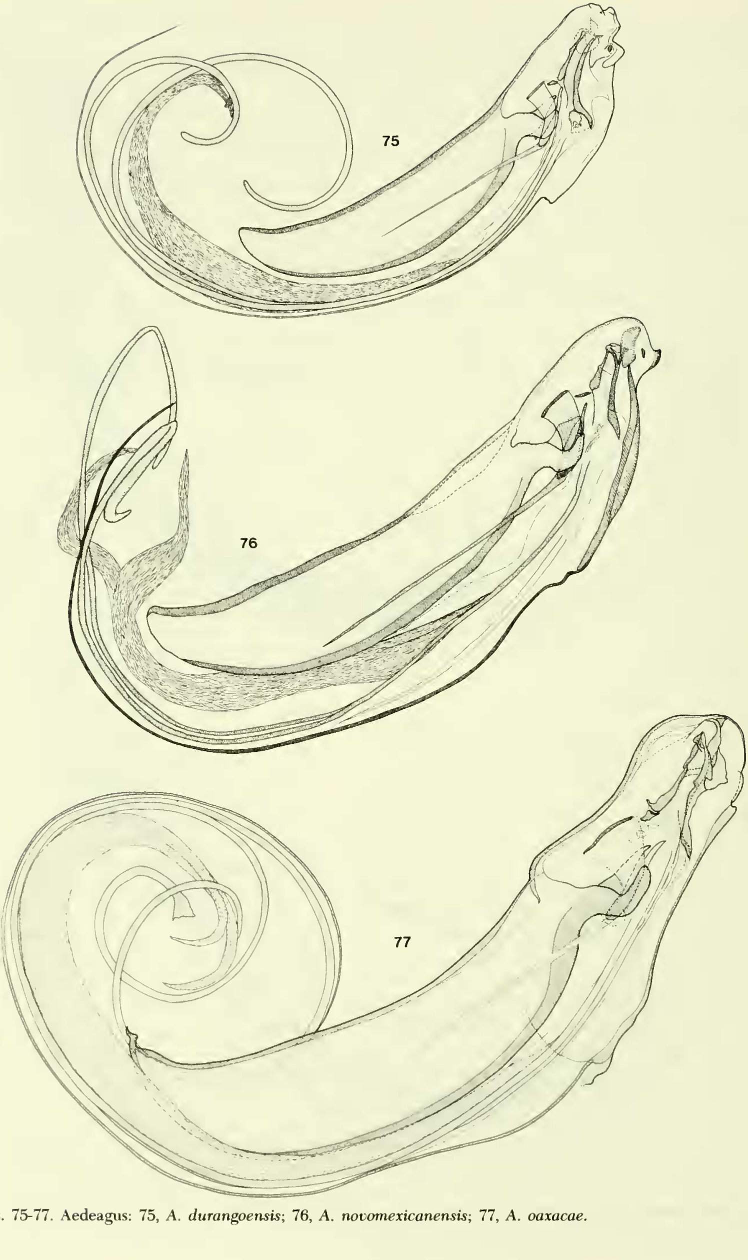
Recorded distribution: California: Monterey Co. (type locality), San Luis Obispo Co. (Linsdale and Davis).

New distribution: From Santa Ynez Mountains of Santa Barbara Co. north to Siskiyou Co., thence south to the western Sierra Nevada foothills to Tulare Co., California.

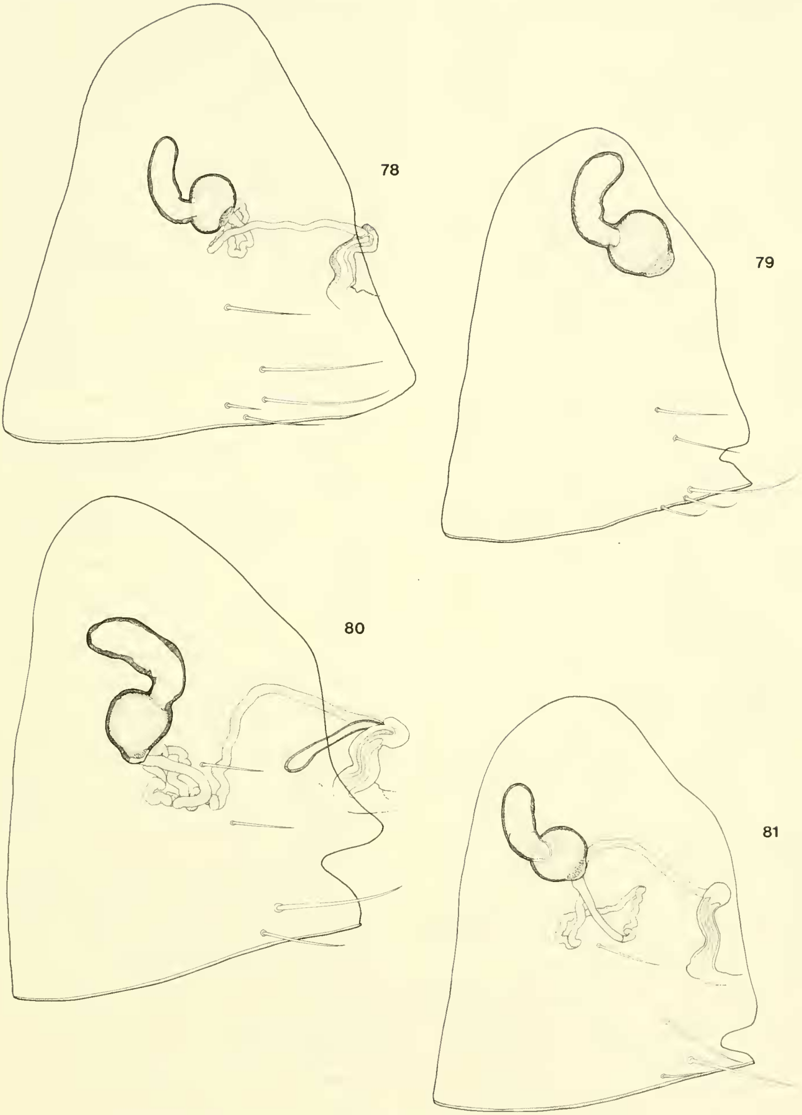
Material examined: California: Alameda Co.: 1 male, 1 female, ex *Neotoma fuscipes*, Oakland (oak woodland), 1 July 1936 (RM); 27 males, 43 females, ex *Neotoma fuscipes* nests, Berkeley (oak woodland), 17 October 1959, Barnes (BVC). Amador Co.: 1 male, 3 females, ex *Neotoma fuscipes* nest, 1.6 km N, 5 km E of Plymouth (oak woodland), 14 January 1959, Barnes (BVC). Contra Costa Co.: 3 males, 7 females, ex *Neotoma fuscipes* nests, Orinda (oak woodland), 18 October 1959, Barnes (BVC). El Dorado Co.: 27 males, 43 females, ex *Neotoma fuscipes* nest, Placerville vicinity (oak woodland), many dates, Barnes (BVC); 110 males, 110 females, ex *Neotoma fuscipes* nest, Shingle Springs vicinity, many dates, Barnes (BVC). Fresno Co.: 4 males, 10 females, ex *Neotoma fuscipes* nest, 3 km N, 2 km W of Auberry (oak woodland), 7 January 1958, Barnes (BVC); 2 males, 6 females, ex *Neotoma fuscipes* nest, 1.6 km SW of Prather (oak woodland), 13 November 1958, Barnes (BVC). Lassen Co.: 1 male, 4 females, ex *Neotoma fuscipes* nest, 5 km NW of Little Valley (oak, *Ceanothus*, sagebrush), 6 May 1960, Barnes (BVC). Monterey Co.: 1 female, ex *Neotoma fuscipes*, Hastings Nat. Hist. Res., 14 July 1938 (RM); 1 male, 2 females, ex *Neotoma fuscipes*, 4 km E of Carmel, 21 December 1948, Holm (BVC); 1 female, ex *Eutamias merriami*, Hastings Nat. Hist. Res., 8 February 1947 (PHS); 1 male, ex *Perognathus californicus*, same locality, 18 January 1947 (PHS). Napa Co.: 1 male, ex *Neotoma fuscipes*, 4 km N, 2 km E of Calistoga (oak woodland), 24 October 1956, Murray (BVC). Nevada Co.: 3 males, 9 females, ex *Neotoma fuscipes* nest, 19 km S of Grass Valley (oak woodland), 15 January



Figs. 73-74. Aedeagus: 73, A. *falsicalifornicus congruens*; 74, A. *falsicalifornicus falsicalifornicus*.



Figs. 75-77. Aedeagus: 75, *A. durangoensis*; 76, *A. novomexicanensis*; 77, *A. oaxacae*.



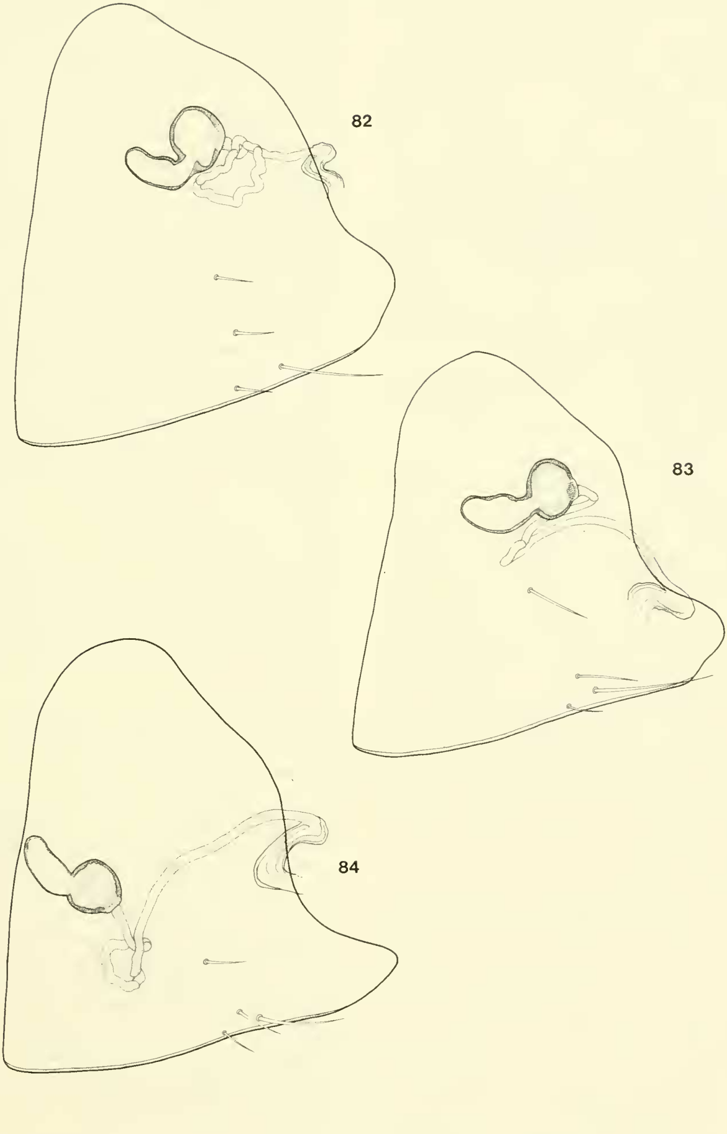
Figs. 78-81. Female seventh sternum and spermatheca: 78, *A. nidiophilus*; 79, *A. sinuatus*; 80, *A. amphibolus*; 81, *A. montanus*.

1959, Barnes (BVC). Plumas Co.: 17 males, 33 females, ex *Neotoma fuscipes* nest, 3 km W of Virgillia, 17 October 1961, Barnes. San Benito Co.: 2 males, ex *Neotoma fuscipes*, T14S R6E Section 2, 13 February 1951, Kirkwood (BVC). San Francisco Co.: 1 male, ex *Spermophilus beecheyi*, San Francisco (laboratory), no date (PHS). San Luis Obispo Co.: 7 males, 19 females, ex *Neotoma fuscipes* nest, 5 km N, 7.2 km E of Santa Margarita (oak woodland), 2 November 1956, Barnes (BVC); 1 male, 5 females, ex *Neotoma fuscipes*, 1.6 km N, 6 km E of Santa Margarita (oak woodland), 15 June 1956, Barnes (BVC); 1 male, 1 female, ex *Neotoma fuscipes*, same locality (oak woodland), 5 March 1957, Barnes (BVC); 1 male, 5 females, ex *Neotoma fuscipes*, 1.6 km N, 6 km E of Santa Margarita (oak woodland), 1 November 1956, Murray (BVC); 1 male, 6 females, ex *Neotoma fuscipes* nest, 5 km N of Pozo (chaparral, woodland), 20 November 1956, Barnes (BVC); 3 males, 1 female, ex *Neotoma fuscipes*, La Panza Camp (chaparral), 3 June 1955, Murray (BVC); 1 male, 1 female, ex *Neotoma fuscipes*, San Luis Obispo, 1 June 1935 (RM); 1 male, ex *Peromyscus boylei*, 1.6 km N, 4 km E of Santa Margarita (oak woodland), 15 June 1956, Murray (BVC); 1 male, 2 females, ex *Peromyscus truei*, same locality (oak woodland), 15 June 1956, Murray (BVC); 1 male, ex *Peromyscus truei*, 3 km N, 6 km E of Pozo (chaparral), 7 March 1957, Barnes (BVC); 1 female, ex *Microtus californicus*, 3 km E of Cayucos, 1 June 1947, Ryan and Durham (HF). San Mateo Co.: 1 female, ex *Neotoma fuscipes*, La Honda, 26 March 1949, Prince (PHS). Santa Barbara Co.: 3 males, 4 females, ex *Neotoma lepida*, Buckhorn Canyon, 6 km E of Santa Maria (chaparral), 24 April 1957, Barnes, Murray (BVC); 1 male, ex *Neotoma fuscipes*, Lompoc (oak woodland, chaparral), 9 February 1961, Rohe (BVC); 31 males, 53 females, ex *Neotoma fuscipes* nests, same locality, 9 February 1961, Rohe (BVC); 11 males, 18 females, ex *Neotoma fuscipes* nests, 47 adults reared from larvae 9 km N, 11 km W of Santa Barbara (oak, chaparral), 8 May 1961; 43 males, 74 females, ex *Neotoma fuscipes* nests, San Marcos Pass, 12 km N, 13 km W of Santa Barbara (oak woodland), 8 May 1961, Barnes. Santa Clara Co.: 1 male, 1 female, ex *Neotoma fuscipes*, Los Gatos, 24 June 1936 (RM). Santa Cruz Co.: 2 males, 1 female, ex *Neotoma fuscipes* nest, Boulder Creek, 305 m, 30 May 1939, Good (BVC); 1 male, 5 females, ex *Neotoma fuscipes*, same locality, 4 July 1940, Good (PHS). Siskiyou Co.: 2 males, 7 females, ex *Neotoma fuscipes* nest, 5 km W of Dorris (oak, pine), 6 April 1960, Barnes (BVC); 3 males, 6 females, 8 km S, 10 km W of Gazelle (juniper, oak), 2 April 1960, Barnes (BVC). Tulare Co.: 1 male, 2 females, ex *Neotoma fuscipes* nest, 1 km N, 5 km E of Lemon Cove (oak woodland), 2 April 1959, Barnes (BVC). Tuolumne Co.: 8 males, 17 females, ex *Neotoma fuscipes* nests, La Grange, 11 March 1958, Barnes and Keh (BVC).

Discussion: Stewart (1940) described *A. congruens* as a full species related to *A. falsicalifornicus*. Hopkins (1952) reduced *congruens* to subspecific status under *falsicalifornicus*, but his reasons weren't given. Linsdale and Davis (1956) presented a substantial case for full specific status for *A. congruens*, demonstrating constant morphological differences between the two forms. Hopkins and Rothschild (1962) held to the view of Hopkins (1952) and kept *congruens* at the subspecific level.

The view of Hopkins is amply supported by morphological, distributional, and reproductive data from this study. This, with the perspective gained from study of the genus as a whole, calls for subspecific assignment of *congruens*.

Morphologically, males of *A. f. congruens* and *A. f. falsicalifornicus* are immediately separable by the shape of the distal arm of sternum IX. In all of the *f. congruens* examined, this structure was narrow and angulate, truncate apically. In *Anomiopsyllus f. falsicalifornicus*, this structure is broader and gently rounded at the apex (Fig. 31). In the south coastal area of California where distributions of the two forms nearly meet, sternum IX of *f. congruens* has two large spiniform setae at the apex and *f. falsicalifornicus* has only one spiniform of moderate size with occasionally a small tacklike seta



Figs. 82-84. Female seventh sternum and spermatheca: 82, *A. nudatus hiemalis*; 83, *A. nudatus mexicanus*; 84, *A. nudatus nudatus*.

immediately below it. In the central Sierra Nevada Mountains populations of *f. congruens*, the number of apical spiniforms on this structure is reduced until, finally, in Tulare County, there are none in some local populations. Specimens with three spiniforms on the finger are occasionally found in more northern coastal populations. The shape of sternum IX remains constant.

Since Fox's (1926) description of *falsicalifornicus* and Stewart's (1940) description of *congruens*, the shape of the movable process has been considered diagnostic for the two groups. Stewart's description of *congruens* emphasized the lack of an apparent distal dilation of the process that he had observed in *falsicalifornicus*. In reality, the apparent dilation is due to a broad concavity of the posterior margin of the movable process, below which there is a broad, lightly sclerotized lobe (Figs. 12, 16). This concavity occurs to some degree in both *f. congruens* and *f. falsicalifornicus*. There is a tendency for more concavity in the process of *f. falsicalifornicus*, but some specimens of *f. congruens* are as deeply concave. A number of authors have erred in drawing and describing this structure, including Fox (1926), Stewart (1940), and Hubbard (1947). These authors failed to include the proximal lobe, an oversight that changes the appearance of the structure considerably. Linsdale and Davis (1956) simply did not illustrate its lower portion. Wagner (1936) illustrated the structure correctly, as did Collins (1936) in his supplementary description of *falsicalifornicus*. The overlap in shape of the movable process reduces its importance as a taxonomic character.

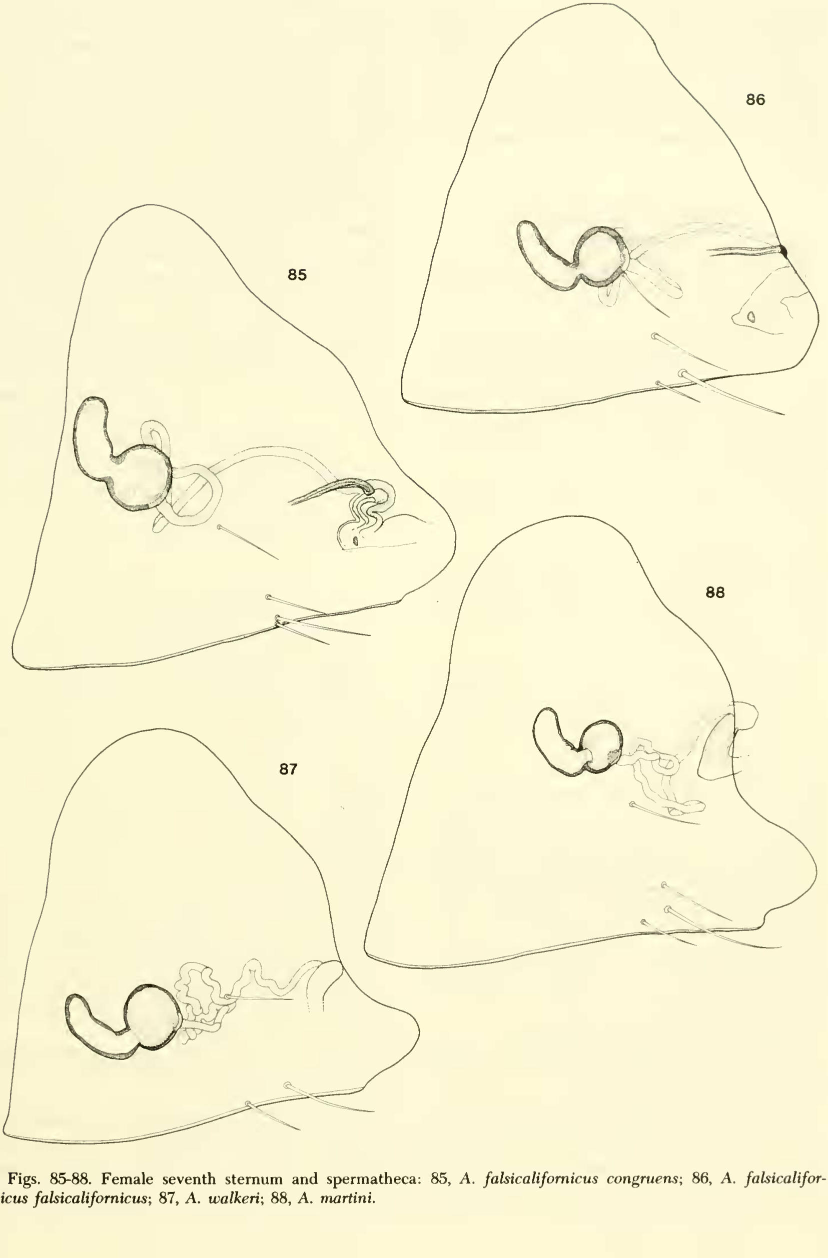
The number and placement of the distal spiniforms were considered to be important by Linsdale and Davis (1956) in distinguishing these two forms. In 73 specimens of *f. congruens* from the type locality, 36 had a full complement (three distal, one proximal on both sides), 19 had one proximal missing on one side, 7 had one proximal moved up near the distal row, and 11 had no proximal spiniforms at all. A series of 17 *f. falsicalifornicus* from Los Angeles had no proximal spiniforms. Of 54 males of *f. falsicalifornicus* examined in the present study, 7 had proximal spiniforms on at least one side and the remainder had none. Of the many *f. congruens* examined, 72 percent had at least one proximal spiniform and 63 percent had proximal spiniforms on both sides. Only an occasional specimen (1 percent) had one or more spiniforms moved up to or near the distal row. The proximal spiniform is evidently in the process of being lost in both forms, but the process has progressed further in *f. falsicalifornicus* than in *f. congruens*. Its presence in some *f. falsicalifornicus* and absence in some *f. congruens* reduces its value as a character.

The fixed process of the clasper is used by Linsdale and Davis (1956) and by Hopkins and Rothschild (1962) to separate *falsicalifornicus* and *congruens*. In material examined in the present study, the general shape was found subject to variation. That of *f. falsicalifornicus* is always longer than broad, and that of *f. congruens* broader than long.

In females, sternum VII varies in contour within populations both in regard to breadth of the ventral lobe and depth of the posterodorsal sinus. The sinus varies from prominent in some specimens to absent in others. The range of variation is completely overlapping between the two subspecies.

The posterior margin of the female tergum VIII has been used to separate species by Hopkins and Rothschild (1962). In *f. falsicalifornicus*, there is considerable variation in its shape. Specimens of *f. congruens* from coastal California may or may not possess a dorsal lobe. Often there is no production of the posterodorsal margin, and rarely does this lobe exceed the ventral production of tergum VIII. Consequently, the sinus between these lobes is either very shallow or absent. Specimens of *f. congruens* from the Sierra Nevada foothills show a definite, broad posterodorsal lobe of tergum VIII which extends beyond the ventral portion of the tergum forming a broad, shallow sinus. Females of *f. falsicalifornicus* from Los Angeles County differ only slightly from coastal *f. congruens* in this respect.

One of the oddities found by the study of many specimens, particularly *f. congruens*,



Figs. 85-88. Female seventh sternum and spermatheca: 85, *A. falsicalifornicus congruens*; 86, *A. falsicalifornicus falsicalifornicus*; 87, *A. walkeri*; 88, *A. martini*.

is that specimens from more humid, coastal areas (e.g., Santa Margarita, San Luis Obispo County) are darker, i.e., more heavily pigmented. This character is also found in the wood rat hosts (Hooper 1938) and is used here as a subspecific character, but it has little value as a taxonomic character in fleas.

Anomiopsyllus falsicalifornicus falsicalifornicus Fox

Figs. 14, 37, 60, 72, 86, 95

Anomiopsyllus californicus: Fox, 1926 (nec Baker, 1904), Pan-Pacific Ent. 2: 183; Wagner, 1930, Mag. Parasitol. Moscow 1: 35.

Anomiopsyllus falsicalifornicus: Fox, 1929, Ent. News 40: 218; Collins 1936, Ent. News 40: 137; Hubbard, 1947, Fleas of western North America: 78-80; Jellison, Locker, and Bacon, 1953, Index to the literature of Siphonaptera of North America, Suppl. 1: 10; Linsdale and Davis, 1956, Univ. Calif. Publ. Zool. 54(5): 306-308; Holland, 1965, Canadian Ent. 97: 1052; Barnes, 1965, Pan-Pacific Ent. 41(4): 278; Jellison and Glesne, 1967, Index to the literature of Siphonaptera of North America, Suppl. 2: 13-19; Coultrip et al., 1973, J. Med. Ent. 10(3): 306.

Anomiopsyllus falsicalifornicus falsicalifornicus Hopkins, 1952, J. Wash. Acad. Sci. 365; Knudsen, 1956, Bull. South. Calif. Acad. Sci. 55(1): 1-6; Hopkins and Rothschild, 1962, Catalogue of the Rothschild Collection of Fleas III: 402-403; Holland, 1965, Canadian Ent. 97: 1053; Lewis 1974, J. Med. Ent. 11(2): 154.

Diagnosis: The males of *A. falsicalifornicus falsicalifornicus* are distinguished from *A. f. congruens* by the shape of the distal arm of sternum IX and the fixed process of the clasper being longer than broad. Sternum IX is two to three times as broad mesally as in *f. congruens* and has the apex gently rounded and equipped at its posterior margin near the apex with one or two stout setae. The movable process is similar to *f. congruens* but lacks the proximal spiniform setae.

Female characters are not sufficiently distinctive to separate subspecies of *falsicalifornicus.*

Type data: That of the species.

Recorded distribution: California: Claremont, Los Angeles County, west to Beverly Glen, Los Angeles County.

Material examined: California: Kern County: 3 males, 4 females, ex *Neotoma lepida*, Poso Creek, 3.5 km S, 8.8 km W of Granite Station, 23 May 1957, (BVC 1781). Los Angeles Co.: 6 females, ex *Neotoma fuscipes*, Sepulveda Canyon, Los Angeles, 11 November 1941, G. Augustson (HF41-148c); 3 males, 7 females, ex *Neotoma fuscipes*, Beverly Glen, June 29, 1941, G. Augustson (HF41-45 GA); 4 females, ex *Neotoma fuscipes*, Los Angeles, 27 April 1941, G. Augustson (HF41-45 GA); 1 female, ex *Neotoma fuscipes*, same locality, 16 November 1940, G. Augustson (HF40-146 GA); 3 males, 3 females, ex *Neotoma fuscipes*, Sepulveda and Mission Roads, 5 May 1959, D. Rohe (BVC 15754); 2 males, 3 females, ex *Neotoma fuscipes*, 4 km N of Bel Air, 17 November 1959, Murray and Rohe (BVC 14703); 17 males, 27 females, ex *Neotoma fuscipes* nests, plus 33 females, 14 males reared from larvae, Sepulveda and Mission Road, 28 March 1962, D. Rohe; 1 male, 4 females, ex *Neotoma fuscipes* nest, Malibu Creek Cornell, 9 May 1961, A. Barnes; 11 males, 19 females, ex *Neotoma fuscipes* nests, San Gabriel Canyon, 13.2 km N of Azusa, 17 December 1956, A. Barnes.

Anomiopsyllus walkeri Barnes

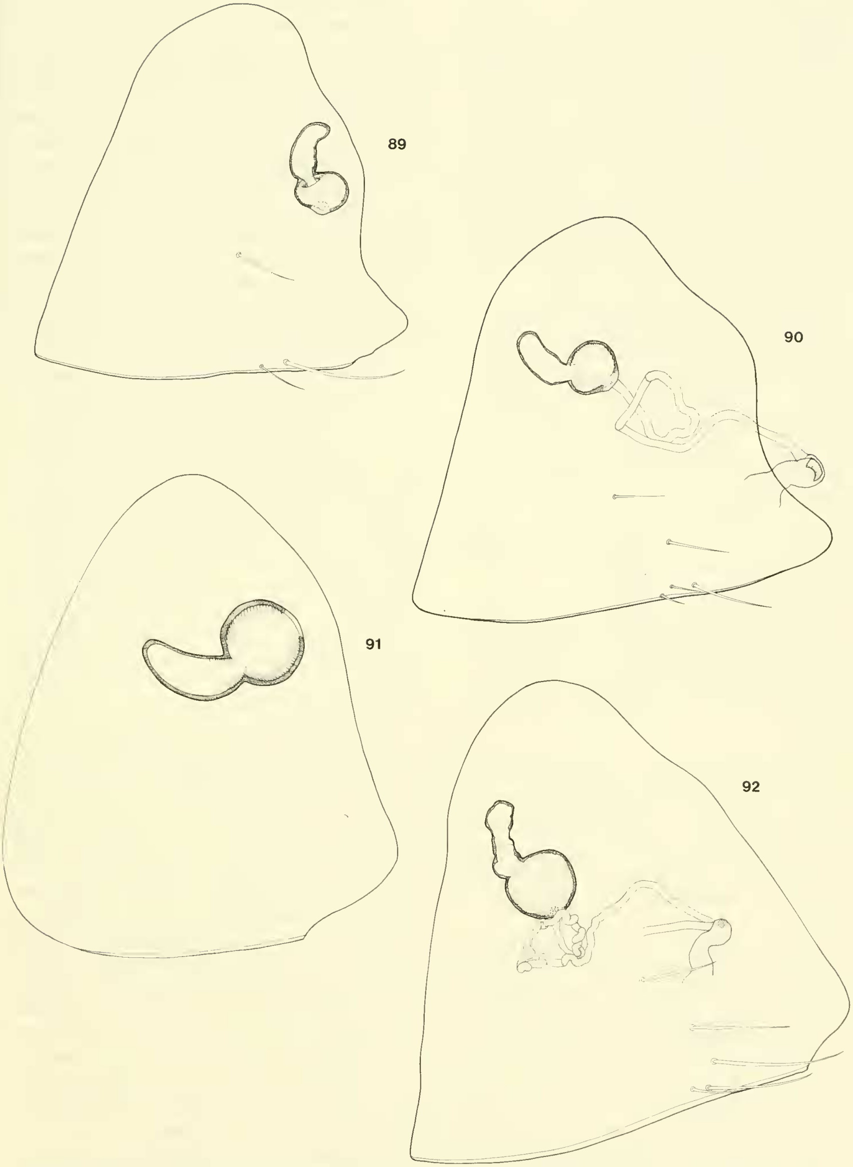
Figs. 13, 38, 59, 74, 87, 94

Anomiopsyllus walkeri Barnes, 1965, Pan-Pacific Ent. 41(4): 272-280; Lewis, 1974, J. Med. Ent. 110: 154.

Diagnosis: Barnes (1965) indicated that *A. walkeri* was related to *A. nudatus*, but may be distinguished on the basis of four spiniforms on the movable process of the clasper with three on the distal portion and one on the proximal portion. Since Holland's description of *A. martini*, it would appear that *walkeri* would be more closely related to *martini* than *nudatus*. The aedeagus of *A. walkeri* differs markedly from *nudatus* in that *walkeri* has a heavily sclerotized dorsal margin and a well-defined dorsomedian "hump" above and slightly anterad to the aedeagal struts. The neck of the aedeagus curves ventrad from the longitudinal axis and the apodeme curves dorsad.

Female characters are not sufficiently distinctive to separate *walkeri* from *nudatus* and *martini*.

Type locality: Male holotype, female allotype from 11 km S, 9 km E of Tehachapi, Kern Co., Calif., ex *Neotoma fuscipes* nest, 19 February 1959 (Barnes). Designated



Figs. 89-92. Female seventh sternum and spermatheca: 89, *A. durangoensis*; 90, *A. novomexicanensis*, 91, *A. traubi* (redrawn from Barrera 1951 and Barnes 1963); 92, *A. oaxacae*.

paratypes: California: Kern Co., 7 males, 19 females, 19 February 1959, 2 females, 2 April 1959; 22 males, 30 females, 22 January 1960; 1 male, 8 females 10 km SE of Tehachapi, 19 February 1959; 7 males, 8 females, 3 km NW of Keene, 18 February 1959; 2 males, 3 females, 3-6 km SW of Glenville, 17 February 1959; 2 males, 1 female, 3 km N, 1 km W of Weldon, 16 March 1960; 5 males, 13 females, 5 km E of Lake Isabella, 18 March 1960. Tulare Co., 2 males, 2 females, 8 km S, 10 km W of Little Lake (Inyo Co.).

Type host: Neotoma fuscipes

Type specimens: The male holotype and female allotype are in the U.S. National Museum. Paratypes are in the following collections: University of California, Berkeley; Bureau of Vector Control, California Department of Public Health, Berkeley, California; British Museum (Natural History), Tring, Hertfordshire; Rocky Mountain Laboratory, Hamilton, Montana; U.S. Public Health Service Field Station, San Francisco, California; private collection of Dr. Robert Traub, Bethesda, Maryland.

Discussion: Barnes (1965) draws attention to the close morphological and distributional relationships between *A. walkeri* and *A. nudatus*, but provides ecological data which supports retention of *walkeri* as a full species.

Anomiopsyllus walkeri replaces *A. nudatus* in the Tehachapi and southern Sierra Nevada Mountains of California. This type of replacement is typical of *Anomiopsyllus* species distribution, with no instance known of two *Anomiopsyllus* species inhabiting the same nest, or even the same wood rat colony.

The area of contact between the two species was examined with this in mind. Special attention was given to the possibility of morphological intergradation and to the habitats in which the two species were found. Substantial numbers of wood rat (*N. fuscipes*) nests were collected from the type locality and adjacent areas during the winter and spring of 1959 and 1960. Fleas were removed from nests by means of a modified Berlese funnel and were examined. Habitat notes were taken along with notes on weather conditions at the time of collection.

The type locality of *A. walkeri* is on the east slope of Double Mountain, the easternmost peak of the Tehachapi chain, and is at 1463 m to 1585 m. The dominant vegetation consists of juniper (*Juniperus occidentalis*) and Joshua tree (*Yucca brevifolia*) woodland, sagebrush (*Artemisia* sp.) and several species of *Eriogonum*. This vegetation characterizes a desert habitat in that area. Such habitats usually have some persistent snow (at least in patches) during midwinter. The average annual rainfall is approximately 30 cm. In the south, alluvial fans slope into Antelope Valley. The plain, which is relatively flat, slopes gradually from about 1067 m in the west to 762 m in the south and east. The valley is largely under cultivation, but on the alluvial fans and in the remaining natural areas on the valley floor juniper-Joshua tree woodland also exists as habitat for *N. fuscipes* along with creosote bush (*Larrea tridentata*), a shrub characteristic of moderate elevation and gentle slopes in the Mojave Desert. Rare winter snows do not persist even for a day in Antelope Valley or on the slopes of Double Mountain below 1220 m. Average annual precipitation is 13 cm at Lancaster and 16 cm at Mojave, two nearby weather stations on the valley floor.

Nest collections were made at and near the type locality on slopes at lower elevations and in Antelope Valley on 19 February 1959; 1-2 April 1959 and on 22 January 1960. A total of 51 nests was collected, with 34 containing fleas, of which 24 contained *Anomiopsyllus* spp., either *walkeri* or *nudatus*. *Anomiopsyllus walkeri* alone was removed from 11 of 22 nests collected at 1402 m or above in juniper-Joshua tree woodland. *Anomiopsyllus nudatus* alone was removed from 13 of 29 nests collected in juniper-Joshua tree-creosote bush at 1280 m or below. A total of 31 male *walkeri* was collected at the higher elevations, and 52 male *nudatus* from the lower. The females were not considered since they are indistinguishable. No evidence of morphological intergradation was found.

It appears that *A. walkeri* is better adapted to areas having some persistent winter snow and higher rainfall. *Anomiopsyllus nudatus* is better adapted to lower elevations characterized by no winter snow, much less rainfall, and the occurrence of creosote bush. In neither case is the rainfall great. It must be pointed out that the rainfall in the habitat of *walkeri* is roughly twice that for the valley below, where *nudatus* occurs.

Competitive exclusion in the zone of contact may occur between *Anomiopsyllus nudatus* and *A. walkeri* in the larval stage, when both species occupy the same nest. Further evidence of this competitive exclusion between *A. nudatus* and *A. walkeri* is noted when analyzing the collection data outside their zone of contact. *A. nudatus* has been collected elsewhere in California from wood rat hosts and nests far above the winter snow line at elevations up to 2287 m, and in areas with average annual precipitation up to 89 cm or more (e.g., Big Bear, California, with a 94 cm annual average). Collections of *nudatus* in the Sawtooth and Liebre Mountains near Sandburg, south of Antelope Valley, and near Desert Springs, San Bernardino County, California, were made in habitats characteristically occupied by *walkeri* in the zone of contact. *Anomiopsyllus nudatus* is never found within the range of *walkeri*.

In view of the morphological differences and the lack of intergradation at a point of close contact, *A. walkeri* must be considered a full species related to *nudatus*. These con-

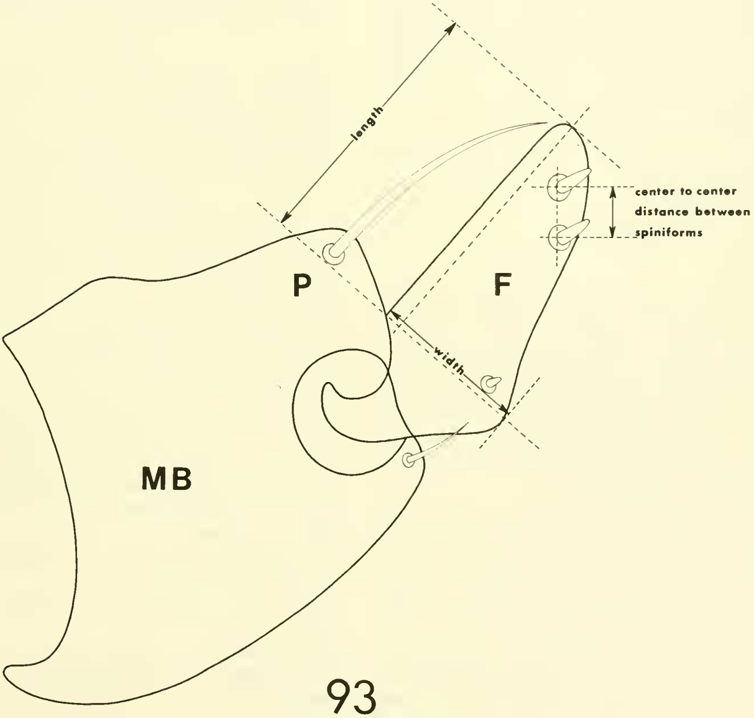


Fig. 93. Diagram of clasper showing measurements used on features of the movable process in the *nudatus* group. All measurements made by means of calibrated eyepiece grid.

siderations further suggest that *walkeri* has evolved in isolation from *nudatus* and has subsequently been brought into contact with the parent species.

Anomiopsyllus martini Holland

Figs. 16, 39, 61, 73, 88, 95

Anomiopsyllus martini Holland, 1965, Canadian Ent. 97: 1054-1056; Tipton and Mendez, 1968, Pacific Insects 10(1): 179; Lewis, 1974, J. Med. Ent. 11(2): 154.

Anomiopsyllus princei Barnes, 1965, Pan-Pacific Ent. 41(4): 276-278 (new synonomy); Haas et al., 1973, J. Med. Ent. 10(3): 282.

Diagnosis: Anomiopsyllus martini has been considered a close relative of *A. nudatus* and *A. walkeri* (Holland 1965, Barnes 1965). The males can be separated by the presence of four spiniforms on the movable process rather than three as in *nudatus* and from *walkeri* by two long, closely placed thick bristles at the arc of curvature of sternum IX. *Anomiopsyllus martini* also differs from *walkeri* in that it has only three heavy setae on the apex of sternum IX, whereas *walkeri* has a fourth smaller seta.

Female characters are not sufficiently distinctive to separate *martini* from *nudatus* and *walkeri*.

Type locality: 16 km W of El Salto, Durango, Mexico, 2744 m.

Type host: Nest of *Sciurus aberti* Woodhouse.

Type specimens: Male holotype and female allotype, 55 male and 59 female paratypes on slides, and 187 male and 207 female paratypes in alcohol collected on 21 June 1964 in a hollow in a dead pine tree; 3 male and 2 female paratypes, same data, but in another tree, on 11 July 1964 by J. E. H. Martin and deposited in the Canadian National Museum.

Discussion: The recorded geographical distribution of this species is limited to two collections: one from El Salto, Durango, Mexico, at an elevation of 2744 m, and one from Catron County near Luna, New Mexico, at an elevation of 2195 m. Both collections were from *Sciurus aberti* and its nest. *Anomiopsyllus martini* and *A. durangoensis* are the only species of the genus, of which we are aware, that are not associated with wood rats.

We list *A. princei* Barnes as a synonym of *A. martini* Holland, even though there are some slight differences in the two populations. In both species there are three distal and one proximal spiniforms on the movable process of the clasper, and the distal arm of sternum IX bears three subapical thick bristles with the posterior margin broadly rounded in the middle.

There are several isolated populations of *S. aberti* squirrels associated with stands of yellow pine in Arizona, New Mexico, and Utah. Further collecting is required to determine if the distribution of *A. martini* is consistent with that of its apparent host, *S. aberti.*

Anomiopsyllus durangoensis Holland

Figs. 26, 47, 63, 75, 89, 95

Anomiopsyllus durangoensis Holland, 1965, Canadian Ent. 97: 1056-1058; Lewis, 1974, J. Med. Ent. 11(2): 154.

Diagnosis: Anomiopsyllus durangoensis is apparently sympatric with *A. martini* but associated with *Peromyscus* sp. Holland (1965) indicated that *A. durangoensis* is closely related to *A. amphibolus* (males) in that both have a triangular-shaped movable process with two spiniforms, but in *durangoensis* both spiniforms are distal. On this basis *durangoensis* would appear to be more closely related to *A. novomexicanensis*, *A. traubi*, and *A. oaxacae*, which possess only distal spiniforms, whereas *A. amphibolus* also possesses one proximal and one distal spiniform. The distal arm of sternum IX is truncate to subtruncate and bears three short, heavy apical setae; the remaining ventral two-thirds bears fewer and thinner setae than in *martini* and *A. n. hiemalis.*

Female characters are not sufficiently distinctive to separate *durangoensis* from *martini* or *n. hiemalis.*

Type locality: 5 km W of Durango, Durango, Mexico, 1982 m.

Type host: Mouse nest (possibly *Peromyscus* sp.)

Type specimens: Male holotype and female allotype, 11 male and 12 female paratypes collected on 24 June 1964 in a nest in a yucca plant by J. E. H. Martin and deposited in Canadian National Museum.

Discussion: The known geographical dis-

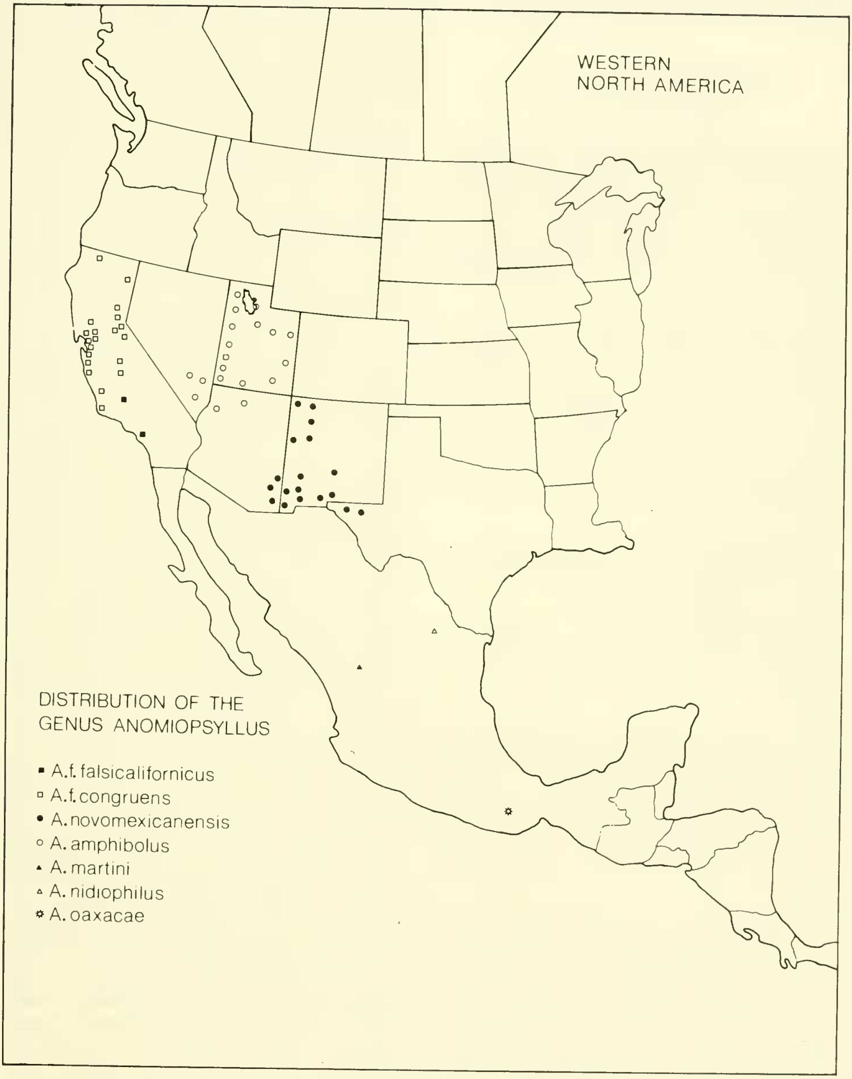


Fig. 94. Map showing the distribution of *Anomiopsyllus* species.

tribution is limited to the type locality near Durango, Durango, Mexico. Intensive collecting in Arizona and New Mexico may reveal the presence of *A. durangoensis*.

Anomiopsyllus novomexicanensis Williams and Hoff

Figs. 27, 49, 62, 76, 90, 95

Anomiopsyllus novomexicanensis Williams and Hoff, 1951, Proc. U.S. Nat. Mus. 101(3278): 307-309; Traub and Hoff, 1951, Amer. Mus. Nov. 1530: 3-4; Vargas, 1960, Med. Rev. Mexicana 40(849): 4; Holland 1965, Canadian Ent. 97: 1053; Jellison and Glesne, 1967, Index to the literature of Siphonaptera of North America, Suppl. 2: 13-19; Rail et al., 1969, J. Med. Ent. 6(1): 93; Miller et al., 1970, J. Med. Ent. 7(6): 698; Graves et al., 1974, J. Med. Ent. 11(4): 490-497.

Diagnosis: Anomiopsyllus novomexicanensis, though similar in many taxonomic characters to the *nudatus* group, is placed with *A. traubi* and *A. oaxacae* on the basis of having only distal spiniforms. *Anomiopsyllus novomexicanensis* males can be distinguished from other *Anomiopsyllus* species by the loss of the long bristle on the fixed process of the clasper.

Females are readily identified from other *Anomiopsyllus* species by the presence of a prominent comma-shaped sclerotization in a portion of the bursa copulatrix.

Type locality: 9.7 km E of Albuquerque, Bernalillo County, New Mexico.

Type host: Neotoma micropus canescens Allen.

Type specimens: Male holotype and female allotype, 332 male and 605 female paratypes collected on 10 October 1948; 62 male and 126 female paratypes on 28 February 1948; 16 male and 4 female paratypes in December 1947 by L. A. Williams and C. C. Hoff, deposited in U.S. National Museum.

Material examined: Arizona: Cochise Co.: 1 male, 1 female, ex *Neotoma lepida*, 19 km W of Bowie on Tucson Rd., 914 m (cactus), 11 October 1938 (PHS); 1 female, ex *Neotoma lepida*, 8 km SW of San Simon, 914 m (cactus), 13 October 1938 (PHS); 1 male, ex *Neotoma lepida*, 9 km S of Bowie, 974 m (cactus), 15 October 1938 (PHS). Graham Co.: 3 males, 3 females, ex *Neotoma lepida*, 32 km NW of Duncan, 1128 m (grass), 28 February 1939 (PHS); 1 male, ex *Neotoma lepida*, 32 km E of Safford, 975 m (cactus), 5 October 1938; 1 male, ex *Neotoma lepida*, 24 km S of Safford on Bowie Rd., 1113 m (cactus), 6 October 1938 (PHS); 1 female, ex *Neotoma lepida*, 38 km NW of Duncan, 1128 m (grass), 1 March 1939 (PHS); 2 females, ex *Neotoma lepida*, 24 km E of Safford, 1067 m (grass), 4 October 1938 (PHS); 1 female, ex *Neotoma lepida*, 40 km S of Safford on Bowie Rd., 1128 m (cactus), 8 October 1938 (PHS); 1 female, ex *Neotoma lepida*, 45 km NW of Duncan, 1128 m (grass), 2 March 1939 (PHS). Greenlee Co.: 3 males, ex *Neotoma lepida*, 6 km SE of Duncan, 1097 m (grass), 4 March 1939 (PHS); 1 male, ex *Neotoma lepida*, 13 km SE of Duncan at N. Mexico line, 1113 m (grass), 6 March 1939 (PHS); 1 male, 1 female, host unknown (*Onychomys leucogaster capitulatus*?), no locality, 2 December 1938 (PHS). *New Mexico:* Bernalillo Co.: 1 female, ex *Neotoma micropus*, 10 October 1948, L. Williams (RM); 3 males, 3 females, ex *Neotoma albigula*, 24 km W of Albuquerque, (juniper, cactus–range), 16 May 1939 (PHS); 4 males, 4 females, ex *Neotoma* sp., 10 October 1948, L. Williams (RM); 24 males, 1 female, ex *Neotoma canescens*, Albuquerque, 10 October 1948, Williams and Hoff; 1 male, 1 female, ex *Neotoma canescens*, Albuquerque, 28 February 1948, Williams and Hoff. Dona Ana Co.: 2 males, 2 females, ex *Neotoma albigula*, 16 km W of Las Cruces, 1097 m (cactus, mesquite–desert), 15 April 1939 (PHS); 3 males, 3 females, ex *Neotoma albigula*, 11-16 km W of Hatch, 1280 m (yucca, grass), 12 May 1939 (PHS); 1 female, ex *Neotoma albigula*, 8-11 km S of Hatch, 1280 m (chaparral), 10 May 1939 (PHS); 1 female, ex *Neotoma albigula*, 3-6 km S of Salem, 1280 m (mesquite), 11 May 1939 (PHS); 1 female, ex *Neotoma albigula*, Las Cruces, February 1939 (PHS); 1 female, ex *Onychomys leucogaster*, 11-16 km W of Hatch, 1280 m (grass), 12 May 1939 (PHS); 1 female, ex *Dipodomys ordii*, 16 km W of Las Cruces, 1097 m (cactus–desert), 15 April 1939 (PHS). Grant Co.: 3 females, ex *Neotoma albigula*, 19 km NE of Lordsburg, 1372 m (cactus, mesquite), 12 April 1939 (PHS). Hidalgo Co.: 1 male, 4 females, ex *Neotoma albigula*, 19-22 km

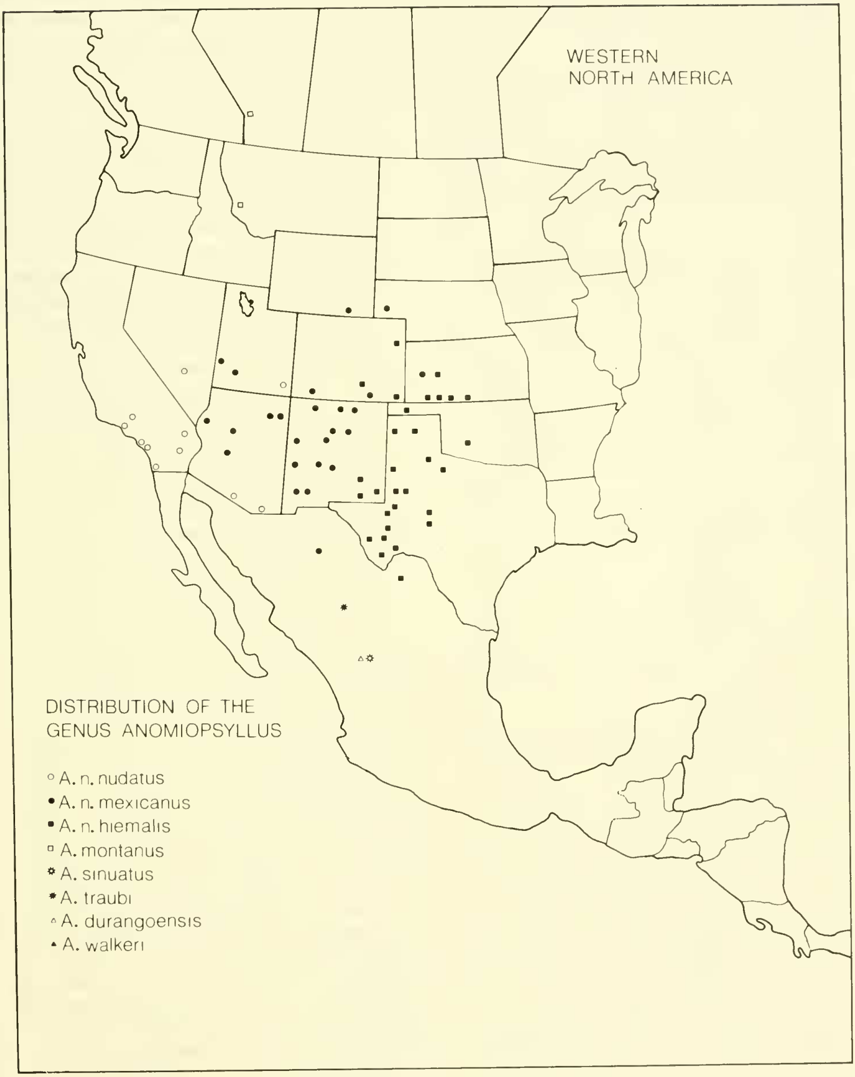


Fig. 95. Map showing the distribution of *Anomiopsyllus* species.

NW of Lordsburg, 1292 m (cactus), 11 April 1939 (PHS); 2 females, ex *Neotoma albigula*, 4.8 km S of Lordsburg, 1292 m (brush), 14 April 1939 (PHS); 5 males, 5 females, ex *Neotoma* sp., 23 km NW of Lordsburg, 1292 m (mesquite), 8 April 1939 (PHS); 1 male, 1 female, ex *Neotoma lepida*, 21 km N of Rodeo, 1341 m (cactus), 20 October 1938 (PHS); 2 males, 2 females, ex *Neotoma lepida*, 32 km N of Rodeo, 1402 m (cactus), 21 October 1938 (PHS); 2 males, 2 females, ex *Neotoma lepida* nest, 8 km N of Rodeo, 1341 m (cactus), October 1938 (PHS); 1 female, ex *Peromyscus maniculatus*, 32 km N of Rodeo, 1402, (grass, cactus), 21 October 1938 (PHS). Lincoln Co.: 1 male, 2 females, ex *Neotoma albigula*, 6 km NE of Carrizozo, 1646 m (yucca), 15 April 1949 (PHS). Luna Co.: 2 males, 5 females, ex *Neotoma albigula*, 5 km E of Deming, 1372 m (chaparral), 2 May 1939 (PHS); 2 males, 2 females, ex *Neotoma albigula*, 5-8 km S of Deming, 1372 m (chaparral), 5 May 1939 (PHS); 1 female, ex *Dipodomys ordii*, 5-8 km N of Deming, 1372 m (yucca, mesquite), 6 May 1939 (PHS). Otero Co.: 1 male, 1 female, ex *Neotoma albigula*, 10 km E of La Luz, Lincoln Nat. Forest, 1372 m, 22 March 1949 (PHS); 1 male, 1 female, ex *Neotoma albigula*, 11 km NE of La Luz, Lincoln Nat. Forest, 1463 m, 24 April 1949 (PHS); 1 male, 1 female, ex *Neotoma albigula*, 4 km E of Tularosa, 1524 m, 25 March 1949 (PHS). Rio Arriba Co.: 1 female, ex *Neotoma albigula*, 3 km SW of Espanola, 1982 m (grass, sage, cactus), 30 May 1939 (PHS). Sandoval Co.: 2 males, 3 females, ex *Neotoma mexicana*, 3 km E of Bernalillo, 1524 m (juniper, sagebrush), 23 July 1949 (PHS); 1 male, 4 females, ex *Neotoma albigula*, 8 km NW of Bernalillo, 1585 m (sage, juniper), 18 May 1939 (PHS). San Juan Co.: 1 male, 1 female, ex *Neotoma albigula*, 8 km SE of Aztec, 2134 m (juniper), 28 May 1949 (PHS). Sierra Co.: 1 male, 1 female, ex *Neotoma albigula*, 32 km N of Engle, 1280 m, 24 March 1949 (PHS); 2 males, 2 females, ex *Neotoma albigula*, 13 km E of Hot Springs, 1280 m, 25 March 1949 (PHS); 1 male, 3 females, ex *Neotoma albigula*, 19 km S of Hot Springs, 1220 m (cactus, sage—desert), 19 April 1939 (PHS); 1 female, ex *Neotoma albigula*, 8-10 km S of Hillsboro, 1555 m (sage, mesquite—plateau), 28 June 1939 (PHS). Socorro Co.: 4 males, 7 females, ex *Neotoma albigula*, 5 km N of Bernardo, 1433 m (grass, sage, mesquite—range), 12 May 1939 (PHS); 4 males, 4 females, ex *Neotoma albigula*, Abo-Pass, 10 km W of Schoole, 1738 m (grass, oaks, juniper), 11 May 1939 (PHS); 2 males, 2 females, ex *Neotoma albigula*, 3 km SW of San Antonio (range), 6 May 1939 (PHS); 1 male, 4 females, ex *Neotoma albigula*, 3 km N of Escondida, 1433 m (near irrigated crops—gravel banks), 2 May 1939 (PHS); 1 male, 1 female, ex *Neotoma albigula*, 16 km W of Socorro, 1524 m (grass, sage—range), 4 May 1939 (PHS); 1 male, 5 females, ex *Neotoma albigula*, 16 km E of San Antonio, 1372 m (sage, cactus—range), 5 May 1939 (PHS); 2 females, ex *Neotoma albigula*, 7 km N of Polradera, 1463 m (sage, mesquite), 3 May 1939 (PHS); 1 female, ex *Neotoma albigula*, 12 May 1939 (PHS); 1 female, ex *Neotoma albigula*, 3 km W of Socorro, 1402 m (cactus, mesquite—range) 2 May 1939 (PHS). Valencia Co.: 4 males, 5 females, ex *Dipodomys merriami*, 3 km W of Belen, 1463 m (grass, sage—dump grounds), 9 May 1939 (PHS); 1 female, ex *Neotoma albigula*, same locality, 1463 m (grass, sage—dump grounds), 9 May 1939 (PHS); 2 females, ex *Neotoma albigula*, 13 km W of Belen, 1524 m (juniper, sage—range), 9 May 1939 (PHS); 1 female, ex *Neotoma albigula*, 31 km W of Hoshunas, 1494 m (sage—range), 10 May 1939 (PHS); 1 female, ex *Neotoma albigula*, 24 km S of Correo, 1524 m (sage, juniper), 25 April 1939 (PHS); 1 male, ex *Peromyscus truei*, 12.9 km W of Belen, 1524 m (juniper—range), 9 May 1939 (PHS); 1 male, ex *Peromyscus boylei*, Harrington Ranch, 1524 m (sage, juniper), 26 April 1939 (PHS). *Texas:* Hudspeth Co.: 1 female, ex *Neotoma*, 19 September 1940 (RM); 3 males, 1 female, ex *Neotoma* nest, Allamore, 19 September 1940 (RM). Culberson Co.: 2 males, 2 females, ex *Neotoma albigula*, 31 March 1942 (PHS).

Discussion: In their remarks following the description of *A. novomexicanensis* Williams and Hoff (1951) grouped this species with *A. n. hiemalis* on the basis of its having three spiniforms on the movable process. They considered the genus to contain two species groups: those with two such spiniforms (i.e., *A. amphibolus*) and those with three (i.e., *nudatus hiemalis*). *Anomiopsyllus falsicalifornicus* with four (usually) was not mentioned.

Characteristics of the fixed process included in the diagnosis are not found in *Anomiopsyllus* species and would apparently place *A. novomexicanensis* in a monotypic species group. The shape, articulation, and adornment of the movable process in *novomexicanensis* would seem to indicate its closeness to *A. traubi* and probably place it in the group which includes *A. traubi* and *A. oaxacae.*

Hosts: Anomiopsyllus novomexicanensis has been collected from four wood rat hosts: *Neotoma albigula, N. micropus* (type host), *N. mexicana,* and *N. lepida stephensi.* Occasional hosts include *Peromyscus, Dipodomys,* and a few sciurids with about the same infestation rate as for other *Anomiopsyllus* species. There were 52 wood rat collections in the material examined, of which *N. albigula* predominated (33), followed by *N. lepida stephensi* (15), *N. micropus* (4), and *N. mexicana* (1). The known range of *A. novomexicanensis* falls within the distribution of *N. albigula* and *N. mexicana,* but occupies only a small portion of either. The collection records for *N. lepida* are all from eastern Arizona. The distribution of *N. micropus* does not extend west beyond New Mexico (Hall and Kelson 1959). As is undoubtedly the case with other *Anomiopsyllus* species for which considerable data exist, the distribution of *A. novomexicanensis* is limited by factors other than that of host distribution.

Distribution and habitat (Fig. 95): The known distribution of *A. novomexicanensis* includes most of southern and central New Mexico, a small portion of southeastern Arizona (Greenlee and Graham counties) and the westernmost corner of Texas (Culberson and Hudspeth counties). To the north and west its distribution interdigitates with that of *A. nudatus mexicanus* and to the east (Texas) with *A. nudatus hiemalis.*

Collection records, where habitat clues and elevations are given, show that *A. novomexicanensis* is a flea of the Chihuahuan

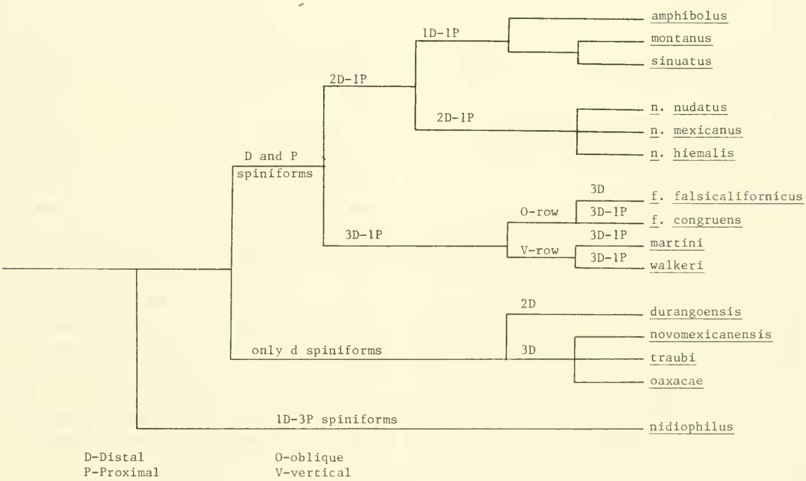


Diagram 1. Cladogram illustrating the relationships of species and subspecies in the genus *Anomiopsyllus*, based on the spiniforms of the movable process on the clasper.

biotic province. It occupies the desert plains and the arid grassland-mesquite belt mentioned by Bradt (1932) and Benson (1933). It also inhabits the low wastelands where its hosts occur, but it primarily occupies the Chihuahuan roughlands belt of Blair (1940) and the lowest edges of the pinyon-juniper belt (sabinal belt of Dice 1942) at elevations of 1220 to 1524 m. Extreme southern New Mexico in Luna, Dona Ana, and Otero counties, where *novomexicanensis* is the only *Anomiopsyllus* recorded, also falls within the Chihuahuan province (Dice 1943). Elements of the Chihuahuan desert interdigitated with portions of the Colorado plateau to the north (Dice 1943, Fenneman 1931). Here, *A. novomexicanensis* is found at lower elevations and *A. n. mexicanus* at higher elevations. Of 52 collections of *novomexicanensis*, 94 percent were made below 1577 m (x = 1357 m), but 83 percent of the *A. n. mexicanus* collections were made above 1524 m and 72 percent above 1692 m (x = 1829 m).

Further evidence that *novomexicanensis* occurs primarily in the lower desert habitats is offered by clues to vegetation type in Public Health Service collection records. These records, where available, have been included in the collection data under material examined. References to cactus, yucca, and mesquite are much more common to the Chihuahuan province where *novomexicanensis* occurs, and references to pinyon, juniper, and sagebrush are much more common to the Colorado Plateau where *A. n. mexicanus* occurs.

Differences in habitat occupied by the two species are probably dependent on two factors: (1) climate, particularly humidity or available moisture as in the observed habitat division between *A. falsicalifornicus* and *A. nudatus nudatus* or between *n. nudatus* and *walkeri*, and (2) competitive exclusion resulting from two related species utilizing the same host niche. Altitudinal overlap in the records shown here may be explained on the basis of differences in microclimate brought about by slope exposure, rain shadow, and precipitation pattern.

Anomiopsyllus traubi Barrera

Figs. 28[6], 48[6], 91[6], 94

Anomiopsyllus traubi Barrera, 1951, Ciencia, 12(6-9): 197; Vargas, 1960, Med. Rev. Mexicana, 40(849): 1-4; Hopkins and Rothschild, 1962, Catalogue of the Rothschild Collection of Fleas III: 401-402; Holland, 1965, Canadian Ent. 97: 1054; Lewis, 1974, J. Med. Ent. 11(2): 154.

Diagnosis: A. traubi males can be distinguished from *A. novomexicanensis* and *A. oaxacae* in that the distal arm of sternum IX has 5-7 stout apical setae. The posterior margin of sternum IX is bare except for a subbasal row of 5-7 long, stout bristles intermixed with long, slender bristles and a single submedian seta. The movable process is broadly triangular and rounded at the posteroventral angle containing a row of three spiniforms placed vertically along the posterior margin.

Type locality: Cueve de Belen, near Zimapan, Hidalgo, Mexico.

Type host: Nest of rodent.

Type specimen: Male holotype collected on 2 November 1950 by A. Barrera, deposited in Alfredo Barrera's collection.

Discussion: Barnes (1963) examined only two male paratypes of this species: one provided by William L. Jellison and one provided by Robert Traub. These specimens had been mounted in Hoyer's mounting medium, and the exoskeletons were fractured by shrinkage of the medium, resulting in the destruction of a number of characters of taxonomic value, particularly in the aedeagus. Hopkins and Rothschild (1962) believe *A. traubi* to be most closely related to *A. novomexicanensis*, but the fixed process of *A. novomexicanensis* is unique in the genus whereas that of *traubi* is most like *A. oaxacae*. The distal arm of sternum IX in *traubi* and *oaxacae* differ by virtue of the subbasal angle of the posterior margin of this structure. The true relationships of *traubi* and *oaxacae* will remain uncertain until additional specimens are available.

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[6] Figures 28, 48, and 91 were redrawn from Barrera (1951) and Barnes (1963). The aedeagus and sternum VIII of the male were not illustrated because of the lack of a specimen.

Anomiopsyllus oaxacae Barnes

Figs. 29, 50, 64, 77, 92, 95

Anomiopsyllus oaxacae Barnes, 1965, Pan-Pacific Ent. 41(4): 278-279; Lewis, 1974, J. Med. Ent. 11(2): 154.

Diagnosis: Barnes (1965) indicated that *A. oaxacae* is most closely related to *A. f. falsicalifornicus* but very different from that species and all other species of *Anomiopsyllus* in that it possesses more and generally longer bristles. *Anomiopsyllus oaxacae* is probably closer to *A. traubi* than to *f. falsicalifornicus*, based on the presence of only distal spiniforms on the movable process in *A. traubi*, whereas *f. congruens* still retains a proximal spiniform. The movable process is broad almost to the point of being rectangular in shape and is equipped with three mesad spiniform setae parallel to the posterior margin of the process. The proximal arm of sternum IX is similar to that of *f. falsicalifornicus*, but the distal arm is long, narrow, and almost parallel sided and armed apically with two posterad rows of heavy, spikelike setae. The posterior margin of the distal arm has a row of 20 evenly spaced, long, thin bristles extending from the base of the lowest apical seta to three-fourths of the distance of the arm. The aedeagal hood extends anterad far beyond the aedeagal struts, and the length of the hood is about equal to the length of the apodeme beyond the anterior margin of the hood.

Length: 1.7 mm.

Type locality: 3 km SE of Matatlàn, Oaxaca, Mexico

Type host: Baiomys musculus (Merriam)

Type specimen: Male holotype collected on 24 July 1953 by R. H. Baker, deposited in U.S. National Museum.

Discussion: This species was described from a single male specimen that was loaned to the senior author by Traub and was originally noted as new by Traub. This specimen represents the southernmost record for the genus. Thus, the range of *Anomiopsyllus* extends into tropical America from whence it reaches northward to Banff, Alberta, Canada. Although *Baiomys musculus* is the type host, the normal host is probably *Neotoma mexicana*, the distribution of which includes Oaxaca, Mexico.

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